WOODCOCK ECOLOGY AND MANAGEMENT

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WOODCOCK ECOLOGY AND MANAGEMENT

Papers from the Seventh Woodcock Symposium held at The Pennsylvania State University, University Park, Pennsylvania, 28–30 October 1980

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Technical Coordinators

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Dedicated to Roger M. Latham, 1914–1979

This Seventh Woodcock Symposium is dedicated to Roger M. Latham, whose contribution to the wildlife profession in general and to woodcock management in particular is widely recognized. He rose to national prominence both as a writer and a professional conservationist. His articles appeared in numerous outdoor-oriented publications in addition to his regular columns in the *Pittsburgh Press*. The Symposium was held in central Pennsylvania where Roger rekindled interest in woodcock at a time (1951) when studies and management of the bird were at an all-time low. This foresight led to the improvement of the status of woodcock in Pennsylvania and helped awaken interest in the bird nationwide.

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Foreword

The papers in this symposium proceedings provide the most up-to-date information on the ecology and management of the American woodcock. This is the seventh in a series of symposiums and workshops on the American woodcock that have been held since 1966. Through this progression of meetings, dedicated groups of biologists and administrators have provided a regular forum for information exchange on a species whose popularity as a game bird is steadily increasing. Research and management reports given at these meetings have evolved from informal general presentations to high-quality scientific papers. Papers in this publication follow the precedent set by the Sixth Woodcock Symposium in that they were formally refereed before being accepted.

The Seventh Symposium was international in scope, with participants attending from Canada, Ireland, Great Britain, and West Germany. Research reports on the European woodcock published in these proceedings enable comparison of two related species whose habitat preferences and social systems are quite different.

Forest management and land-use trends could possibly be the most important factors affecting future woodcock populations. A special session with invited papers, held the second day of the symposium, provides the most recent information available on these topics. Several additional papers deal with on-site management of woodcock habitat and provide practical methods to enhance woodcock populations at the local level.

The success of any symposium on wildlife can only be measured by the positive research or management programs that it fosters. The 1980's will undoubtedly see new pressures on wildlife and their habitats. Future research should continue to contribute knowledge on the biological and ecological characteristics of woodcock as a basis for understanding its relations with its environment, particularly the effects of habitat alterations and management practices and the impact of human exploitation on population dynamics. The results of this symposium should be of great benefit in providing support for new and ongoing programs to safeguard this important game bird.

Many individuals and organizations deserve recognition for their efforts in making this symposium a success. The symposium planning committee included Robert Wingard, Terry Rader, Gerald Storm, James Wakeley, Stephen Liscinsky, Richard Coon, Thomas Dwyer, and John Tautin. William L. Sipple, Jr., arranged for the use of the J. O. Keller Conference Center at The Pennsylvania State University and made arrangements for the field trip. The Port Matilda Sportsman's Federation and most notably one member, Mike Ondik, did an excellent job of hosting the banquet. Robert Butler, former leader of the Cooperative Fishery Research Unit at the Pennsylvania State University, provided an outstanding carving of a female woodcock and chick as an award for the best paper; Susan Sutherland contributed a pen-and-ink sketch of an American woodcock for the second place award in the contest. Walter Tzilkowski supervised the flawless operation of the projection equipment and, with James Hudgins, coordinated the shuttle bus system. Session chairmen included James Wakeley, Glen Sanderson, Dale Sheffer, Robert Bond, Stephen Liscinsky, Gene Wood, and John Harcus. Dorothy Detwiler assisted in preparing manuscripts for publication. Finally, the Accelerated Research Program for Migratory Shore and Upland Game Birds and the Office of Migratory Bird Management made funds available to publish these proceedings.

David L. Trauger, Chief
Division of Wildlife Ecology Research

Frontispiece. Pen and ink sketch of nesting American woodcock by Susan Sutherland.

The American Woodcock: A Keynote Address

by

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Some years ago I saw a skit in which a ditty was sung entitled "You are only a blip on the oscilloscope of life." During the time span when humans have interacted with the American woodcock, the blips of enlightenment regarding this species have varied in time and intensity. What follows is the woodcock oscilloscope as I saw it and see it.

It is axiomatic to begin history at the beginning, but the beginning of woodcock history is in part obscured by the use in America of European common names, any one of which could mean woodcock. Some even referred to groups of birds as well as to individuals (Jameson 1909).

The first woodcock referred to by name was recorded as being part of the diet of the Montagnais Indians of Quebec (Le Jeune 1635); however, Lawson's (1714) more detailed account of the bird's size and habitat leaves no doubt that he is talking about the American woodcock in the Carolinas of the 1600's. Thomas Pennant (1784–85) provided the first of the early taxonomic descriptions but failed to present his bird names in Latin. And so it was Johann F. Gmelin, after he prepared and edited, in Latin, the thirteenth edition of Linneaus's *Systema naturae*, who is credited with naming the American woodcock. The scientific binomial changed at least 14 times before it stabilized in our current AOU checklist (Wetmore 1957) as *Philohela minor*. The name is derived from the Greek: *philos* meaning loving and *helos* meaning bog or wet ground. The specific name *minor* refers to the fact that it is smaller than the European woodcock. Thus the taxonomic baptism produced the first major blip on the woodcock oscilloscope.

The individual blips on our screen during that latter half of the 19th century are small but numerous, like a veritable milky way of small contributions on woodcock. Many of these are to be found in the now regrettably defunct sportsman's journal *Forest and Stream*. In the early 1950's, my wife and I began to compile a bibliography on the American woodcock (which we never completed), and we were astonished by the number of citations in that journal. They covered a spectrum of subject matter from behavior to albinism, and a similar gradation spectrum occurred in accuracy and credibility. Nonetheless, the insights in aggregate provided vital information and stimulated inquiry through provocative recording based on limited data. During this same period, under the pseudonym of Frank Forester, H. W. Herbert added luster to the pages of *Forest and Stream* and published numerous books that expressed the sportsman's view of hunting and made substantial contributions to woodcock lore. His sometimes overly elegant victorian prose often overwhelmed the otherwise substantive observations or conclusions.

Large numbers of woodcock seen in the field in the early 20th century and gross daily bags of sports and market hunters were doubtless the result of migrating concentrations during the spring and autumn. It is questionable whether protection from the gun was ever needed, then or now, but it was comforting to know that at the State level, concerned conservationists pressed for harvest restrictions if only to protect local coverts. The Migratory Bird Treaty Act of 1918 gave the Federal government control of the woodcock's welfare. Spring shooting and market hunting became illegal. Bag limits and season restrictions soon followed. These events produced a small but significant blip on the woodcock oscilloscope.

A very enlightening paper by Henry Mousley (1935) appeared under the lengthy title: *A historical review of the habits and anatomy of the woodcock compiled from the earliest drawings and accounts to those of the present day*. This interesting and informative account is as much a personal history of the contributors to woodcock understanding as it is the natural history of the woodcock. Part of this narrative records that a George Cumberland was the first artist to draw the muscle and bone structure of the European woodcock head to illustrate how the bird is able to move its upper mandible without moving the lower. The artist ran off with the wife of the man in whose house he was a boarder and later salved the man's hurt with 1,000 pounds sterling. How these two bits of information relate is vague from a scientific viewpoint, but they illustrate the interlaced vignettes of personal history and science that characterize this contribution.

The anatomical aspects of the eye, ear, and brain are discussed by Mousley along with pterolography, sex and aging, capture, and early art forms involving woodcock, plus anatomical comparisons between snipe and the American woodcock. In spite of the reader not always knowing which species of woodcock was being discussed, the contribution is major.

The next effort virtually lit up our woodcock oscilloscope screen. In my opinion, no woodcock study should be undertaken without first consulting O. S. Pettingill's (1936) study of the American woodcock. It is not only an excellent compendium of woodcock knowledge prior to its publication, it also added to and organized new information on the life history of this bird. Much of the meaning of the data presented (i.e., the ecology of the woodcock) was not adequately discussed, and the monograph was criticized for this omission by Wm. Vogt in *Birdlore* (1936). Linsdale (1936) also leveled some "aroused opinions" on the effort. I have little quarrel with the criticisms by these two reviewers. I would, however, not retreat from my original position that this study be examined as a first step when beginning a research project on woodcock. This study provides much of the basic biology of the species, thus freeing a researcher's time to explore woodcock ecology which draws on the basic biology for relationships and understanding. The Pettingill monograph, in spite of brief lapses in scholarship, is still a classic and, for its day, was ahead of its time.

Howard L. Mendall and Clarence M. Aldous produced the next major blip on the woodcock screen. Their bulletin, entitled *The ecology and management of the American woodcock* (1943), covered some of the same aspects recorded by Pettingill but added new dimensions to the knowledge of woodcock. They used banded birds to determine the relationship of the bird to its environment. The role of management was explored through census, banding, mortality (particularly through hunting), sex ratios, and manipulation of the hunter, the predators, and the habitat itself. In the last instance, the creation of a peenting or singing ground in monotypic cover was a breakthrough in habitat manipulation. The bulletin compares favorably with Pettingill's report 7 years previous, and stands as a model for species management.

In the same year of the Mendall and Aldous contribution there also appeared on the screen a small but important blip in the form of a paper by Frank A. Pitelka (1943) in the *Wilson Bulletin*. It was entitled "Territoriality, display, and certain ecological relations of the American woodcock." Apart from the explicit assessment of ambient conditions associated with the woodcock under observation, the text leans very heavily on previous literature. This research centered on only three established males that were under detailed study for about 40 hours on 11 separate days. No birds were marked. From these data was produced a well written 27-page paper. It is a classic in data squeezing and the astute use of literature. In envy, I confess that I have worked with woodcock for over 30 years, and the results would not require half the number of printed pages. Of course this might surprise no one. The last two lines of his summary read as follows: "American woodcocks may become temporarily established on territories during the period of spring migration."

The import of that statement had a profound effect on road transects and block censusing of peenting birds in spring. Timing to separate local breeders by avoiding migrants is essential to census accuracy.

In 1951 (to 1968) I began a program of wing examination for sex and age of Hungarian partridges (*Perdix perdix*) in Wisconsin. The wings were obtained by sending hunters, who had taken partridges the previous year, prepaid envelopes for wings from birds bagged during a current season. The success of this effort prompted the development of envelopes for Wisconsin woodcock hunters. My project never got beyond the designed envelope because a more sophisticated rangewide program at the Federal level emerged in the same year. Hunting statistics were recorded on the envelope that transported the wings of shot woodcock.

At about the same time, the U.S. Fish and Wildlife Service also organized a rangewide survey of singing (peenting) males along random transects in suitable habitat as an indicator of spring population levels. Among cooperators were State conservation department field personnel who were assigned to follow the Federal guidelines for counting (Anon. 1963). Other agencies and individuals also participated. The wing collections of the hunting season, including the questionnaire data, and the spring peenting counts have given management insight into harvest and population change. The major management efforts resulting from these data are extremely limited. The one reference I found read as follows: "Most states where hunting seasons have previously extended into late February have curtailed their 1975-76 season somewhat" (Artmann 1977). Even here there are several ameliorating qualifiers like "curtailed," "most," and "somewhat."

The still-to-be-resolved aspects of these surveys are (1) when, or at what point in the statistical change of the survey data can we expect action regarding management, and (2) what will that action be? Of the two, the "when" requires valid or even plausible rationale.

Perhaps we have been expecting too much from what are essentially monitoring efforts. It may be doubtful that the accumulated indices are sensitive enough to produce an accurate assessment of change or of the fluctuations recorded, particularly at a rangewide level. The Migratory Bird and Habitat Research Laboratory is examining and adjusting the program to provide answers. This pair of monitoring schemes in spring and fall produced a sizable blip on the woodcock oscilloscope screen. The hope is for an even larger blip in the future.

A rangewide banding program provided a series of interesting capture techniques, but any management resulting from the almost shamefully expensive banding of woodcock created only a minor blip on the woodcock screen.

The brightest flash on the screen in recent years was occasioned by William Sheldon's *The book of the American woodcock* (1967). It is well written and adequately documented. To avoid the criticism of not examining European literature, Sheldon includes a brief section on the European woodcock. The work covers the current woodcock scene in a style and depth to enlighten both layman and biologist, as he adds dimensions of art and pleasing prose to his compilation of pertinent data on this species. The field techniques are given detailed coverage, and he is generous in his acknowledgments of help from colleagues.

This assemblage will recognize the large blip resulting from the birth of this symposium series, namely the first woodcock seminar held in 1966 (subsequent meetings were referred to as "workshops" or "symposia"). The idea for that gathering stemmed from conversations among John Ward, Bill Marshall, and G. Morman Slade (a businessman, a college professor, and a gentleman farmer, respectively). The action resulted when others were also struck with the idea of dramatizing the need for research and research support on the American woodcock. The University of Minnesota and the U.S. Fish and Wildlife Service sponsored that first effort at the Long Lake Conservation Center in northern Minnesota. In the meetings that followed, we have come a long way (and there is a long way still to go), but to these three men and their associates we owe a debt of gratitude for a timely focus on this truly American game bird. These meetings and the enthusiasm they generated played no small part in obtaining Federal support for a research program on "webless migratory game birds" which was funded in the fiscal year 1967-68.

The mid-1900's, like the mid-1800's, produced a blizzard of small but important contributions to understanding woodcock. Each contribution enhanced our knowledge: studies of behavior, broods, habitat relationships, food, blood chemistry, and many others. This symposium and others before it are vehicles to share and to put these efforts into perspective. The oscilloscope responded with a satisfying glow in the 1900's as it did in the middle and late 1800's.

I would like to think that at least a small bump on the oscilloscope line has been produced by the work at the University of Wisconsin. Since 1938 a spring singing-ground census has been made on the 1,100-acre U.W. Arboretum. I was responsible for the census for the past 37 years (except in 1970, when I was on sabbatical in Ireland) with the help of experienced people. Arrival dates have been kept, and a number of special observations and studies have been made in the interim. The ecological changes in the plant cover on the study area have also been noted and aerial photos obtained. These data have not been analyzed,

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but I know of no other comparable census on the same site over a longer time span or where the cover has been mainly unaltered by man.

In the early years of the study, Aldo Leopold and I conducted concurrent censuses – he at his "shack" area 40 miles north of Madison and I at the University Arboretum. Perhaps the blip will be larger when all of these data are analyzed and put in perspective.

For me to attempt to name all the people who have contributed to knowledge on woodcock would be prohibitive in time, and I would run the risk of inadvertently omitting someone. I can think of at least 10 to a dozen more that could rightly be recognized, but the bottom line must be drawn.

The value of each achievement in woodcock ecology will perhaps be assessed differently by the newly initiated, by the seasoned veterans, and by the old-timers among conservationists concerned with woodcock. These groups are also conditioned by who pays the salaries, by group leadership, and by the stated mission that guides their hands and minds.

The day for adding more bits and pieces to a general life history of the woodcock, or any species for that matter, should be over. What we must avoid in our research and ultimately in publication is ending up with results that prompt the question, So what? It is easy for woodcock researchers such as are here assembled to agree with each other and see merit in all studies and thus create a mutual admiration society.

The primary reason for research on woodcock is to provide data that form the basis for assuring the welfare of this species through programs of management. Each effort must define for colleague and layman alike how its results relate to that end.

I have no quarrel with esoteric research that is interesting or exciting and relates only to a scientific data bank or comparative biology. In the field of wildlife management, however, we can afford little such luxury. It does not mean that we avoid "deep-digging" research; it does mean that even deep-digging results should lead to action on behalf of the resource itself – in this instance, the American woodcock.

All animals that are trapped or fall before the gun require the utmost in effort and ingenuity in providing data on which management can safeguard the wildlife resource. Indeed, it is a professional wildlifer's responsibility to strive toward that end.

With current bag limits and season restriction, I do not believe that the harvest can seriously affect the woodcock population. Local overharvest or habitat loss affect the local hunter's bag and his outlook, but the species remains intact.

With more than enough wintering and breeding coverts, and because these coverts rarely conflict with commercial exploitation, only local shortages are obvious. There may come a time when the national harvest will need adjustment to protect the breeding population. There may come a time when land-use practices on a broad scale will negatively affect woodcock well-being on the breeding or wintering grounds.

It is against such contingencies that we undertake to learn all we can of the biology and ecology of woodcock; but we must not initiate, conduct, or justify our field efforts with fancy words and obscure objectives.

Let me leave you with this considered and personal assessment, which may be either sobering or satisfying.

The American woodcock is virtually unaffected by current exploitation. It adapts so well to changes in its breeding and wintering habitats that these environments are not population limiting – I only wish I had proof positive.

If true, does this mean that we stop our investigations on this species because it is looking after itself? On the contrary. The monitoring programs are vital. Violent and unpredicted natural and man-made change can occur at any time. Management of local coverts are as much a concern for wildlife ecologists and managers as are continental woodcock populations. Any research toward those ends should provide safeguards for the species as well as the traditional recreation. If it were otherwise we would not be here this morning.

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Assessment of Some Important Factors Affecting the Singing-Ground Survey

by

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Abstract

A brief history of the procedures used to analyze singing-ground survey data is outlined. Some weaknesses associated with the analytical procedures are discussed, and preliminary results of efforts to improve the procedures are presented. The most significant finding to date is that counts made by new observers need not be omitted when calculating an index of the woodcock population. Also, the distribution of woodcock heard singing, with respect to time after sunset, affirms the appropriateness of recommended starting times for counting woodcock. Woodcock count data fit the negative binomial probability distribution.

Surveys to assess the population status of migratory game birds are a key element in their management. For most species, estimates of population size are derived from expanded counts of individual birds or groups of birds. The counts are usually made along transects or in selected areas where the birds are concentrated. Direct enumeration of a portion of the population to provide a basis for estimating the total works reasonably well for large, conspicuous, and gregarious birds such as waterfowl and cranes. These conventional methods are not suitable for American woodcock (*Philohela minor*) because they are small, solitary, cryptically colored, and occur in dense habitats. Fortunately, male woodcock can be counted readily because of their unique song and conspicuous courtship behavior. Singing males thus serve as the basis for the woodcock singing-ground survey conducted each spring by the U.S. Fish and Wildlife Service (FWS). In contrast to surveys that provide direct estimates of populations, the singing-ground survey provides an *index* of the size of the spring-breeding population.

The singing-ground survey is coordinated by the FWS in cooperation with the Canadian Wildlife Service, 24 States and Provinces, and many individuals. Although various forms of the survey have been conducted in the past, in its present form, singing male woodcock are counted along roadsides each spring on randomly selected, permanent routes in the mid and northern portions of the woodcock's breeding range. About 1,400 singing-ground survey routes exist, and they are almost equally divided between the Eastern and Central management units. The counts are timed to coincide with seasonal and daily peaks in courtship activities. Observers record the number of singing males heard at each of 10 stops along a 3.6-mile (about 6.3-km) route. The average number of singing males per route is used as the index of the breeding population of woodcock.

The Evolution of the Singing-Ground Survey

The present singing-ground survey is the product of a long evolutionary process that began in 1937 when Mendall, Swanson, and Aldous established the first singing-ground route at Moosehorn National Wildlife Refuge in Maine (Mendall and Aldous 1943). Survey techniques evolved in a somewhat haphazard manner through the 1940's and 1950's. Field procedures were finally standardized by the early 1960's. Further improvements were made to the singing-ground survey in the late 1960's, when nonrandom routes were replaced with randomly selected routes. Survey techniques and analytical methods used now are essentially the same as those used in 1970. Generally, the analytical methods were altered as a result of changes in field procedures for counting singing woodcock. That this survey evolved over an interval of 30 to 40 years interferes, to some extent, with the ability to view the historical information as a uniform and comparable picture of trends in the woodcock breeding population.

Present field procedures are sound and practical and, for the most part, result in a satisfactory index. It is unlikely that field procedures will be changed significantly in the future. The evolution of analytical procedures has, however, been less complete. In view of today's standards for monitoring the status of migratory game birds, a thorough assessment of the analytical procedures used in the singing-ground survey is needed. The FWS is now addressing this need and upgrading the analytical procedures. The purpose of this report is to present some preliminary results of the assessment.

An analysis of singing-ground survey data has several features. Most important, and central to the other features, is the former use of "comparable" data to calculate an annual index of the population. Data were considered comparable if the route was surveyed in both the years of comparison by the same observer under similar conditions. Assessment to date has focused on this feature. Before discussing preliminary results of the assessment, it will be useful to briefly review the history of using comparable data and to outline attendant problems.

The Use of Comparable Data

History

The practice of using only comparable data in the analysis was initiated about 1940 by Howard Mendall. At that time the total number of woodcock heard on the routes was used as the population index. To calculate population index changes between years, Mendall used only totals of woodcock heard on routes surveyed in both years that were to be compared. The scope of the survey was then expanding, and this use of comparable data eliminated the obvious bias that would have resulted from including woodcock heard on new routes that were being run for the first time. The practice of using comparable data became more restrictive in the early 1960's following the studies of Goudy (1960) and Duke (1964). These studies resulted in standardized field criteria for counting woodcock and recommendations that data not be used unless the routes were run under similar environmental conditions by the same observers. Consequently, a stringent set of criteria were developed to determine whether count data were acceptable and comparable.

Attendant Problems

The use of comparable data requires two estimates of the population index for any given year: one for calculating the percent change from the preceding year and one for calculating the percent change to the following year (Table 1). Two estimates are needed because the group of data paired with comparable data from the preceding year frequently is not the same group paired with comparable data from the subsequent year. Consequently, a single index value cannot be quoted for a given year. Also, the calculation of a change (trend) among years is complicated.

About 25% of all data are rejected in most years because they are not considered comparable, and this represents a significant loss of otherwise useful data. Failure to run a route in a year and changes in observers are the most frequent causes for rejection. If a route is rejected in either year of the comparison, data for neither year are used. Additionally, there is a partial loss

Table 1. *Sample calculation of between-year changes in the population index.*

Years of comparison	Index year 1	% change	Index year 2	% change	Index year 3	% change	Index year 4
1 and 2	2.36	+ 10	2.60				
2 and 3			2.55	+ 12	2.86		
3 and 4					3.00	+ 7	3.21

of data at the stop level within routes. For example, stops made too early or late are rejected. Only acceptable stops common to both years of a comparison are used. Consequently, routes used in analyses have an average of fewer than 10 stops. Numerous other factors (e.g., start-stop time range, start-stop distance range, time, and distance between stops) and combinations of factors are considered in determining whether or not data are comparable. The complexity of the comparisons requires that many subjective judgements be made. It is difficult to foresee all possible situations and develop objective criteria to cover them.

Assessment of the Use of Comparable Data Preliminary Results

Probability Distribution of Woodcock Count Data

A basic understanding of factors affecting a population index requires knowledge of how the count data are distributed statistically. The probability distribution of singing-ground survey count data was examined by using the total number of woodcock heard on each run of a route as a discrete variable, and various data sets were created by using combinations of states and years. These sets ranged from large (e.g., all states, all years) to small (e.g., all routes run in New York in 1979). A typical distribution of these sets is illustrated in Fig. 1. The variances of these data sets were consistently larger than the means, suggesting that the count data were contagious or clumped and would probably fit the negative binomial distribution. The fit of 25 data sets was tested by using methods outlined in Southwood (1966), and it was concluded that the negative binomial is an appropriate and satisfactory model. In continuing assessments it will be assumed that singing-ground survey count data fit a negative binomial probability distribution.

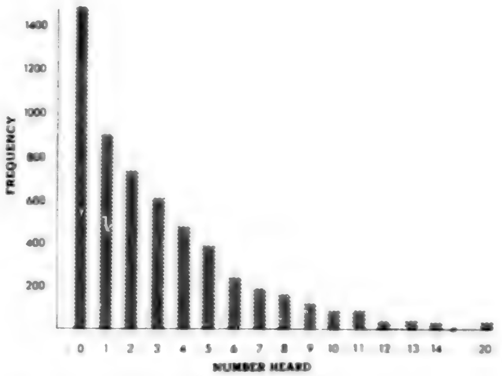

Fig. 1. Frequency distribution of woodcock heard singing on routes run in the Eastern Region, 1968–80.

Effect of Observer Change

About 10% of all routes that were run are not used each year because of observer changes. Real differences in observers' abilities to hear singing woodcock were demonstrated by Duke (1964), and persons familiar with counting singing woodcock can attest to this. Mayfield's (1966) comprehensive work on hearing loss and the ability to hear bird songs provides corroborative information. He reported that at about age 32, men begin to show a distinct and gradually worsening loss of hearing in the frequency range of 4,000 cps and higher. The sound from the peent call of a woodcock is concentrated in the range of 4,000–6,000 cps (Duke 1964; Beightol and Samuel 1973).

Despite strong evidence indicating differences in people's ability to hear singing woodcock, the necessity of rejecting data from routes run by new observers was questioned. It was hypothesized that the differences would be compensatory at the broad regional or rangewide scale (i.e., that some new observers would hear more and others fewer woodcock than their predecessors, with the net effect being nil). An ideal test of this hypothesis would be to compare numbers of woodcock heard by different observers who ran the routes together and recorded their findings separately. Unfortunately, few such situations exist because, although many routes are run by two or more observers, forms are submitted jointly to insure comparability if only one of the observers were to run the route in the following year. The hypothesis was tested by considering both between- and within-year differences in counts by old and new observers. Observers were considered new if someone else had run the route the previous year; old observers were those who had run the same route the previous year.

Between-Year Differences

Differences in the number of woodcock heard

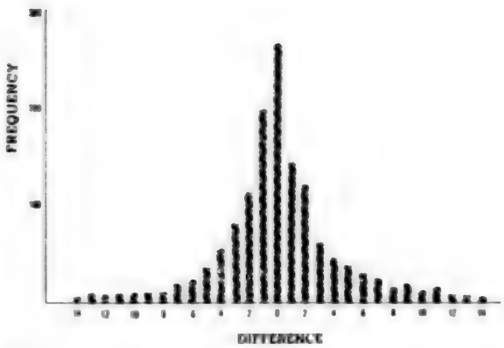

Fig. 2. Frequency distribution of differences in woodcock heard on a route for 2 years when the observer changed.

on a route between two consecutive years were calculated for all instances where the observers changed. The distribution of calculated differences at the rangewide level (Fig. 2) was similar to distributions at the regional level. The null hypothesis that the mean difference equals zero was then tested by using a *t*-test and specifying a rejection region of $P < 0.05$. The null hypothesis was not rejected in any of the tests at either the rangewide or regional level (Table 2).

Testing the mean difference in this simple manner requires the assumption that the effect of population change between years is negligible (i.e., that differences reflect abilities of observers to hear birds and do not reflect population changes). Although it is highly unlikely that this assumption is true for all pairs of consecutive years, the assumption becomes reasonable for the rangewide level if the long-term rangewide population is considered to be stable. To the best of my knowledge, the rangewide population has been stable (Tautin 1979). The assumption is probably not true at the regional level because of long-term population changes within the regions (Tautin 1980). However, only when the null hypothesis was rejected would the effect of population change between years need to be determined.

Within-Year Differences

The effect of observer (old versus new) on numbers of woodcock heard on routes run in the same years was tested by using an analysis of variance. Observer effect was not significant ($P < 0.05$) in any of the analyses for either the rangewide or regional level (Table 3).

Based on the results of these analyses, it was concluded that a change in observers is not a valid or necessary criterion for rejecting singing-ground survey data. These findings and conclusion are consistent with those of Enemar et al. (1978), who postulated that observer bias is insignificant in bird census work done on a large scale. Scale is a key consideration here. If one were analyzing data from one route or a small sample area, then the effect of observer change may be important. However, for management purposes, which emphasize regional summaries and statistics, the FWS will no longer exclude data solely because the observer changed between years.

Times for Starting and Ending Woodcock Routes

Several early workers, including Pettingill (1936), Mendall and Aldous (1943), and Pitelka (1943), reported that woodcock begin evening courtship performances when light intensity is about 21.5 lx (2 fc), a light level that generally occurs within several minutes after official sunset, depending on atmospheric conditions. Courtship performances last about 45 min. Duke (1964) studied the relation between time after official sunset and the onset and cessation of courtship activities and recommended that woodcock counts start 22 min after official sunset (15 min when cloud cover exceeds 75%). His

Table 2. *Test results for the hypothesis that the mean difference between the numbers of woodcock heard in two consecutive years by different observers equals zero.*

	N	$\bar{X}$	SD	t	PR>t
Rangewide	1271	0.043	4.194	0.37	0.713
Eastern Region	529	−0.021	3.456	−0.14	0.885
Central Region	602	0.097	4.725	0.54	0.590

Table 3. *ANOVA results testing effect of observer (old versus new) on the number of woodcock heard on routes within years.*

Source of variation	F value	PR>F
Rangewide		
Observer	2.96	0.0852
Year	3.33	0.0002
Region	53.42	0.0001
Observer-Year Interaction	1.61	0.0878
Observer-Region Interaction	0.03	0.8602
Year-Region Interaction	2.38	0.0062
Observer-Year-Region Interaction	0.88	0.5615
Eastern Region		
Observer	2.26	0.1332
Year	1.20	0.2793
Observer-Year Interaction	1.40	0.1645
Central Region		
Observer	1.00	0.3170
Year	4.38	0.0001
Observer-Year Interaction	1.13	0.3312

study also resulted in the present practice of considering stops as being acceptable for comparisons if they were made between 19 and 57 min after official sunset (12–50 min when cloud cover exceeds 75%).

The appropriateness of these recommended start times and intervals of acceptance was evaluated by plotting mean numbers of woodcock heard per minute after sunset. Ideally, the count at the first stop on a route should begin at the recommended start time, and succeeding stops should be at 3-min intervals (2 min for listening, 1 min for travel). Not all observers start at precisely the recommended time and, for various practical reasons, times between stops are frequently 4 min or more. As a result, most routes, although acceptable, are not run ideally. This variation in start times and stop intervals enabled points outside the range of acceptability to be plotted.

Mean numbers of woodcock heard per minute after sunset were plotted (Fig. 3). Observations from routes run with a recommended start time of 15 min after sunset were adjusted (+ 7 min) and included in the calculation of each point, but stop numbers were disregarded in the analysis. The recommended start time of 22 (or 15) min after sunset appears to be appropriate, and the range of acceptability (19–57 or 12–50 min) appears to be conservative. The variation seen in points at the right end of the plot is most likely a result of small sample sizes (less than 50 observations). For most points, though, sample sizes were large, ranging from several hundred to 8,451 observations for the 22nd minute.

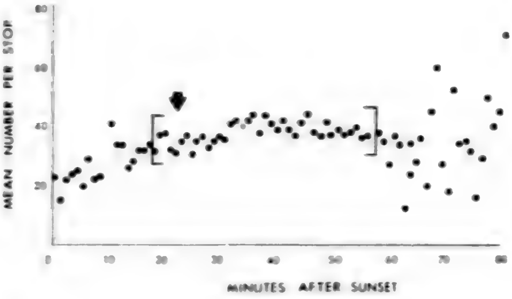

Fig. 3. Mean numbers of woodcock heard singing per minute after sunset. Brackets enclose the range of acceptability. Arrow indicates recommended start time.

Mean numbers of woodcock heard per minute after sunset were also plotted using data only from ideally run routes. As a result, sample size was eliminated as a source of variation, allowing examination of the distribution of woodcock heard calling by stop (Fig. 4). Duncan's multiple range test (Duncan 1955) was used to test for differences among the means per stop; it showed that the mean numbers of woodcock heard on the first three stops were less ($P<0.05$) than all of the others. Consequently, final conclusions cannot yet be drawn regarding start times and acceptance intervals. The potential bias of the differing stop means will be investigated further, and the merits of widening the acceptance range will be considered.

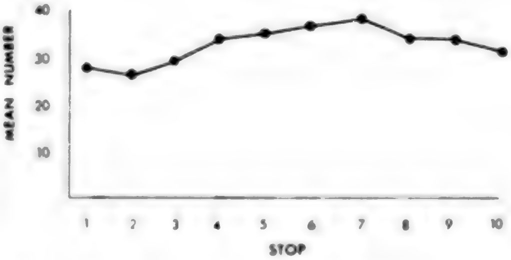

Fig. 4. Mean numbers of woodcock heard singing by stop on ideally run routes. Stops 1, 2, and 3 differ significantly ($P < 0.05$) from the rest.

Summary

Preliminary results of an assessment of procedures used to analyze singing-ground survey data indicate that: (1) woodcock count data fit the negative binomial probability distribution, (2) the numbers of singing woodcock heard by new and old observers do not differ significantly, and (3) recommended starting times for counting woodcock are appropriate. The second finding is of particular importance because it enables a more complete and efficient use of survey data, and it eliminates automatic rejection of data if the observer changed between years. Additional work remains to be done to refine criteria for accepting data to be used in analyses. However, it appears likely that the practice of using only comparable data to calculate an index of the woodcock population will be discontinued.

Acknowledgments

R. Pospahala and R. Blohm provided advice and contributed substantially to all aspects of data analysis and testing. S. Rhoades did much of the necessary computer programming. L. Moyer provided advice on computer programming and the management of data files. B. Galowin provided clerical assistance in all phases of the work.

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Regional Population Inferences for the American Woodcock

by

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Abstract

Woodcock (*Philohela minor*) bandings and recoveries from 1967 to 1977 were analyzed from two large banding reference areas corresponding to existing Eastern and Central harvest units. We examined temporal, age specific, sex-specific, and geographic variation in both survival and recovery rates, using recently developed stochastic models. Survival rate estimates for females were higher than those for males, and higher for adults than for young. There was no significant difference in recovery rates between young and adults. Recovery rates of Eastern unit birds were higher, and overall survival rates were lower than those of Central unit birds. Survival rate estimates were used with crude production rate estimates in a simple modeling effort, and resulting rates of population increase were 1.2 to 1.3 times higher in the Central reference area.

In a recent study (Coon et al. 1977), two harvest units (Eastern and Central) were identified for the American woodcock (*Philohela minor*) in the United States; only 3% of the harvested woodcock from either unit was recovered outside the unit of origin. No regional analysis, however, has yet been published on woodcock survival and recovery rates. Martin et al. (1969) presented survival and recovery rate estimates from winter bandings of woodcock in Louisiana, and the large number of preseason bandings from Maine have also been analyzed (Krohn et al. 1974).

The purpose of the present paper is to present survival and recovery rate estimates from preseason banded woodcock in each of two banding reference areas (corresponding closely to the two harvest units) and to examine potential sources of variation in these rates. Specifically, we examine temporal, age-specific, sex-specific, and geographic variations in both survival and recovery rates. The motivation for this analysis derives from a need to understand woodcock population dynamics in general and to determine whether any regional differences in survival and recovery rates exist in American woodcock. We also estimate production rates and use simple population projection models to further contrast the two banding reference areas.

Data Source and Methods

Banding and recovery information was obtained from the U.S. Fish and Wildlife Service Bird Banding Laboratory, Laurel, Maryland. Sample size limitations generally make it impossible to study population dynamics of birds banded at single banding stations. We therefore combined woodcock bandings from the same general geographic area with similar recovery distribution patterns into banding reference areas. Recoveries of woodcock banded as normal, wild birds during the prehunting season period (1 April to 31 August) and reported shot or found dead during a subsequent hunting season (1 September to 15 February) from 1960 to 1977 were used to define the reference areas. Bandings and recoveries were mapped by degree blocks of latitude and longitude to delineate areas with similar recovery distributions. An Eastern and a Central reference area (one in each harvest unit) were established (Fig. 1), and subsequent analyses were performed on the bandings and recoveries from these areas.

Survival and recovery rates were estimated by using the methods and algorithms developed by Brownie and Robson (1976) and Brownie et al. (1978). Relatively short banding periods are

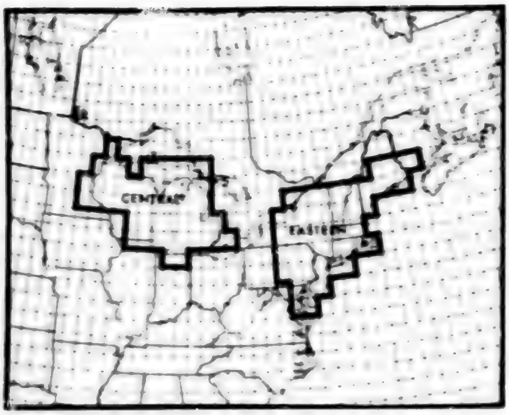

Fig. 1. Location of the Eastern and Central banding reference areas.

highly desirable when these estimation models are used (e.g., see Brownie et al. 1978:184), and thus we used a data set that was more restricted than the one used to establish the reference areas. The banding period for the new data set was defined as the 3-month period extending from 1 May to 31 July. Recoveries were restricted to the hunting season, which we defined as extending from 1 September to 15 February. We also restricted the analysis to birds banded from 1967 to 1977. Reasonably large numbers of annual bandings and recoveries are required by these estimation models, and woodcock bandings before 1967 did not meet the sample-size requirements. We also eliminated all bandings and recoveries from High Island (Whitcomb 1974) in Michigan because that population was subjected to artificially high harvest rates due to the nature of ongoing research there.

We used the series of models in Brownie et al. (1978:56–90), which allow the use of bandings and recoveries from both young and adult birds. All birds banded in their first summer of life are defined as young, and all other birds are defined as adults for purposes of this analysis. Thus, we were able to obtain information on the survival and recovery rates of both age groups and to test for differences between groups.

Hypotheses about variation in survival and recovery rates were tested by using z-test statistics (Brownie and Robson 1974; Brownie et al. 1978:180–182). Small sample size properties of these test statistics are not well understood, but here we followed other workers and assumed that they were approximately distributed as normal (0, 1) under the null hypothesis in each test.

Survival and Recovery Rates

Parameter Estimates

Woodcock banding data are not especially well suited for use with the models of Brownie et al. (1978:185) because of the relatively small sample sizes of bandings (especially of adults), and because of the overall low recovery rates. These problems are reflected by the rather large sampling standard errors associated with the parameter estimates (Tables 1, 2). There is also a considerable difference in the character of the data sets from the Eastern and Central areas; the former set is characterized by larger sample sizes and generally smaller standard errors. Despite these potential problems, the estimates presented in Tables 1 and 2 appear reasonable and represent the best data available for woodcock. We therefore proceeded to investigate sources of variation in survival and recovery rates.

Sex-specific Variation

The mean recovery rate for young females was significantly larger ($P < 0.05$) than that for young males in the Eastern reference area (Table 3). Although this was the only significant difference, the mean recovery rate estimates were larger for females than for males in all four data sets. We computed a composite Z-statistic (composite $Z = \sum_{i=1}^{n} z_i / \sqrt{n}$, where n is the number of individual z-test statistics included in the composite statistic) for all four data sets as $Z = 2.39$, indicating significantly ($P < 0.05$) higher recovery rates for females. We therefore concluded that recovery rates tend to be higher for females than for males, although the magnitude of this difference may vary among age classes and areas and seems to be most pronounced in young birds.

When we consider possible sex-specific differences, it is perhaps important to recall the definition of recovery rate. Recovery rate represents the probability that a banded bird alive at the midpoint of the banding period in year t survives until the hunting season of year t and is then shot and its band reported to the Bird Banding Lab-

Table 1. *Estimates of survival and recovery rates of woodcock banded preseason in the Eastern reference area.*[a]

		Adults				Young			
		Recovery rate		Survival rate		Recovery rate		Survival rate	
Sex	Year	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Male	1967	0.011	0.011	0.494	0.301	0.016	0.011	0.350	0.214
	1968	0.048	0.020	0.490	0.284	0.036	0.014	0.092	0.097
	1969	0.040	0.015	0.512	0.316	0.038	0.013	0.265	0.211
	1970	0.016	0.007	0.280	0.143	0.019	0.008	0.170	0.105
	1971	0.038	0.010	0.247	0.107	0.051	0.010	0.164	0.081
	1972	0.036	0.009	0.362	0.138	0.023	0.007	0.268	0.107
	1973	0.044	0.011	0.208	0.096	0.030	0.007	0.183	0.082
	1974	0.054	0.018	0.237	0.167	0.025	0.009	0.128	0.102
	1975	0.041	0.024	–	–	0.026	0.013	–	–
Mean[b]		0.036	0.005	0.354	0.052	0.029	0.003	0.202	0.048
Female	1967	0.061	0.030	0.174	0.185	0.023	0.013	0.608	0.327
	1968	0.027	0.015	0.907	0.507	0.100	0.032	–	–
	1969	0.020	0.009	0.391	0.188	0.048	0.017	0.083	0.085
	1970	0.043	0.013	0.398	0.178	0.052	0.013	0.231	0.127
	1971	0.034	0.010	0.314	0.117	0.021	0.008	0.348	0.128
	1972	0.034	0.009	0.694	0.235	0.030	0.009	0.530	0.192
	1973	0.029	0.008	0.559	0.269	0.044	0.010	0.351	0.177
	1974	0.038	0.016	–	–	0.048	0.015	–	–
Mean[c]		0.036	0.005	0.491	0.073	0.046	0.007	0.358	0.077

[a] Estimates were obtained from Model H_1 of Brownie et al. (1978:59–64).

[b] Data set included 1,703 bandings and 97 recoveries for adults and 2,876 bandings and 125 recoveries for young.

[c] Data set included 1,368 bandings and 93 recoveries for adults and 1,968 bandings and 130 recoveries for young.

oratory. The approximate midpoint of the woodcock banding period is 15 June, and the hunting season does not begin until September. The apparent difference between male and female recovery rates could therefore be indicative of either of two possibilities: (1) that males and females have similar probabilities of surviving until the hunting season, and that females are more vulnerable to shooting than males, or (2) that females are not more vulnerable to shooting than males, but that their survival probabilities over the 15 June–September period are greater than those of males (see subsequent inferences about sex-specific variation in survival rates). We cannot distinguish between these two possibilities on the basis of available data.

Krohn et al. (1974) examined data for woodcock banded in Maine and concluded there was no variation in recovery rates associated with either age or sex, but they apparently performed no z tests. Their analysis differed from ours in two other respects. The geographic area they used was smaller than our Eastern reference area, and the resultant smaller sample sizes almost certainly resulted in less power to detect true differences. A reexamination of their data base indicated that they included bandings from a large portion of each year (i.e., they used a 6-to 7-month banding period), whereas we chose a restricted banding period, as suggested by Brownie et al. (1978:184).

The null hypothesis (no difference between survival rates for males and females) could not be rejected for any of the four data sets tested (Table 3). The power of these individual tests, however, was quite low (probability to detect a true difference between survival rates of 0.10 with significance level $\alpha = 0.10$ ranged from 0.14 to 0.28) because of the poor precision of the survival estimates. The estimates of mean survival rate were considerably higher (about 0.12) for females among young and adult birds from the Eastern reference area and for adults of the Central area (Table 3). The composite test statistic for young and adults indicated a significant difference in the Eastern area ($Z = 1.83$, $P < 0.10$), which

Table 2. *Estimates of survival and recovery rates of adult and young woodcock banded preseason in the Central reference area.*[a]

		Adults				Young			
		Recovery rate		Survival rate		Recovery rate		Survival rate	
Sex	Year	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Male	1969	0.021	0.021	–	–	0.016	0.016	0.355	0.290
	1970	0.044	0.024	0.352	0.323	0.089	0.023	0.270	0.228
	1971	0.029	0.022	0.992	1.013	0.014	0.010	0.597	0.539
	1972	0.015	0.011	0.247	0.262	0.011	0.006	0.181	0.179
	1973	0.017	0.012	0.340	0.370	0.006	0.004	0.709	0.544
	1974	0.011	0.008	0.077	0.066	0.012	0.005	0.169	0.089
	1975	0.060	0.028	0.689	0.759	0.030	0.011	0.430	0.458
	1976	0.023	0.023	0.106	0.125	0.037	0.014	0.142	0.122
	1977	0.060	0.029	–	–	0.013	0.006	–	–
Mean[b]		0.031	0.007	0.40	0.15	0.025	0.004	0.356	0.124
Female	1969	0.036	0.035	0.195	0.199	0.029	0.029	0.321	0.239
	1970	0.065	0.030	1.182	0.916	0.100	0.030	0.453	0.382
	1971	0.026	0.019	0.597	0.548	0.031	0.022	0.539	0.483
	1972	0.014	0.009	0.324	0.226	0.018	0.010	0.191	0.129
	1973	0.031	0.014	0.822	0.438	0.026	0.010	0.178	0.120
	1974	0.028	0.012	0.169	0.089	0.004	0.004	0.157	0.076
	1975	0.079	0.028	0.609	0.324	0.041	0.018	0.548	0.282
	1976	0.082	0.032	0.304	0.234	0.018	0.013	0.119	0.136
	1977	0.059	0.033	–	–	0.020	0.012	–	–
Mean[c]		0.047	0.008	0.525	0.096	0.032	0.006	0.313	0.094

[a] Estimates were obtained from Model H_1 of Brownie et al. (1978:59-64).

[b] Data set included 549 bandings and 24 recoveries of adults and 2,342 bandings and 86 recoveries of young.

[c] Data set included 563 bandings and 49 recoveries of adults and 1,273 bandings and 64 recoveries of young.

had the most precise parameter estimates, but not in the Central area. The composite test statistic for both age classes in both areas approached significance ($Z = 1.51$, $P = 0.13$). Thus, there was an indication of a difference despite the low power of the tests, and we concluded that the survival rates of female woodcock tend to be higher than those of males.

From recaptures of birds banded in previous years on a Maine study area from 1976–79 (Dwyer, unpublished data), we also have indirect evidence that females live longer than males. Each year the average minimum age (all birds first captured as after-second-year were assumed to be 3 years old) of returning males to the Maine area was 2.1 years, whereas females averaged 2.7 years.

Although female woodcock tend to have higher recovery rates than males and may be more vulnerable to harvest by the gun (if reporting rates and survival from banding until the hunting season are equal between sexes), some aspect of natural mortality in this species must take a much higher toll of males than of females. Alison (1976) presented records of three male woodcock that died in 1975 during an early spring snowstorm in Ontario. Mortality to males on their breeding grounds due to inclement weather early in the breeding season may be common in American woodcock. In the northern part of the breeding range, males arrive before females, often when nighttime temperatures are still below freezing, and undergo the stress of establishing territories and conducting courtship flights when the ground may still be frozen and/or snow covered. During the courtship period, males are at the lowest point in their annual weight cycle (Owen and Krohn 1973; Whitcomb 1974; Dwyer unpublished data) and could therefore be more susceptible to death through starvation during early spring storms. Males are also probably more prone to predation than females because they advertise their presence so conspicuously on their singing grounds (Sheldon 1967).

Table 3. *Results of testing hypotheses regarding sex-specific variation in woodcock recovery and survival rates.*

Reference area	Age	Years	Recovery rates[a] $\dot{f}_F - \dot{f}_M$	Z	P	Survival rates[b] $\dot{\hat{S}}_F - \dot{\hat{S}}_M$	Z	P
Eastern	Adult	1967-74	0.000	0.03	0.97	0.121	1.31	0.19
	Young	1967-74	0.016	2.41**	0.02	0.125	1.28	0.20
Central	Adult	1969-77	0.016	1.42	0.16	0.123	0.70	0.45
	Young	1969-77	0.007	0.92	0.37	-0.044	-0.28	0.78

[a] Results of a z test (Brownie et al. 1978:180-182) testing the null hypothesis that recovery rates for males and females were similar. The difference between the mean annual recovery rates of males and females is denoted by $\dot{f}_F - \dot{f}_M$.

[b] Results of a z test (Brownie et al. 1978:180-182) testing the null hypothesis that survival rates for males and females were similar. The difference between the mean annual survival rates of males and females is denoted by $\dot{\hat{S}}_F - \dot{\hat{S}}_M$.

**$0.01 < P < 0.05$.

Age-specific Variation

Three types of tests were used to investigate possible age-specific variation in survival and recovery rates of woodcock. First, we used the likelihood ratio test of models H_0 vs. H_1, suggested by Brownie et al. (1978:87-89). This basically tests the null hypothesis that both survival and recovery rates are similar for young and adults, versus the hypothesis that survival and/or recovery rates of adults and young differ. This test provided no indication of age-specificity of these parameters among males of either reference area (Table 4). However, the test statistic for Eastern area females indicated significant ($P < 0.10$) age-specific variation, and the statistic for females in the Central area approached significance (Table 4).

We further examined possible age-specific variation through separate tests of the hypothesis that recovery rates and then survival rates differed between ages. The z-test statistics provided no evidence of a consistent difference between recovery rates of young and adults (Table 4). The approximate power of these tests, with respect to a true difference of 0.01, between recovery rates ranged from 0.25 to 0.50. However, the null hypothesis of no difference between young and

Table 4. Results of testing hypotheses regarding age-specific variation in woodcock recovery and survival rates.

Reference area	Sex	Years	Survival and recovery rates[a] df	X^2	P	Recovery rates[b] $\dot{f}_A - \dot{f}_Y$	Z	P	Survival rates[c] $\dot{\hat{S}}_A - \dot{\hat{S}}_Y$	Z	P
Eastern	M	1967-75	18	13.50	0.76	0.007	1.20	0.23	0.151	2.29**	0.02
	F	1967-74	16	25.62*	0.06	-0.010	-1.29	0.20	0.063	0.58	0.56
Central	M	1969-77	17	16.37	0.50	0.006	0.69	0.49	0.043	0.28	0.78
	F	1969-77	17	22.86	0.15	0.015	1.39	0.16	0.212	1.89*	0.06

[a] Results of a likelihood ratio test of model H_0 vs. H_1 (Brownie et al. 1978:88-89) testing the hypothesis that survival and recovery rates were similar for adults and young.

[b] Results of a z test (Brownie et al. 1978:180-182) testing the null hypothesis that recovery rates of adults and young were similar. The difference between the mean annual recovery rates of adults and young is denoted by $\dot{f}_A - \dot{f}_Y$.

[c] Results of a z test (Brownie et al. 1978:180-182) testing the null hypothesis that survival rates of adults and young were similar. The difference between the mean annual survival rates of adults and young is denoted by $\dot{\hat{S}}_A - \dot{\hat{S}}_Y$.

*$0.05 < P < 0.10$.

**$0.01 < P < 0.05$.

adult survival rates was significantly ($P<0.10$) rejected for both Eastern area males and Central area females (Table 4). Mean survival estimates were higher for adults in all data sets, and a composite test statistic over all sets indicated a significant difference ($Z = 2.52$, $P < 0.05$). Thus, we concluded that survival rates of adult woodcock tend to be higher than those of young, although the magnitude of the difference may vary by sex and area.

The conclusion that young woodcock are not recovered at a higher rate than adults is in contrast to the general finding of age-specific vulnerability to hunting for waterfowl species (Anderson 1975). Krohn et al. (1974) concluded that a similar pattern of no age-specific variation in recovery rates existed for preseason banded woodcock from Maine. Goudy et al. (1970) concluded that in the woodcock population of Canaan Valley, West Virginia, immature males were the most vulnerable to shooting, but they apparently did not rely on straightforward tests between pairs of recovery rates to draw this inference, and they noted potential sources of error in their methodology. Again it is important to recall the definition of recovery rate and to remember the importance of June–September survival to its interpretation.

Because overall survival rates are higher for adults, and because recovery rates do not seem to vary with age, young of this species must be subjected to greater natural mortality than adults. We have no information, however, as to when or where this natural mortality occurs (e.g., on the wintering ground or during migration).

Geographic Variation

We computed z-test statistics for each age-sex class to test the null hypothesis that recovery rates were similar for woodcock from Eastern and Central reference areas. The null hypothesis could not be rejected for any age-sex class (Table 5). The approximate power of these tests (corresponding to a true recovery rate difference of 0.01 and $\alpha = 0.10$) ranged from 0.25 to 0.51. The actual mean recovery rate estimates were slightly higher in the Eastern area for three of the four age-sex classes. However, although we computed a composite test statistic over all classes, the null hypothesis still could not be rejected.

A substantial number of bandings in the Eastern reference area came from the Moosehorn National Wildlife Refuge in Maine, where woodcock hunting is prohibited. We therefore eliminated all Moosehorn bandings, computed direct recovery rates, and again calculated z-test statistics for each age and sex class. Only data from 1970 to 1974 could be used in this analysis because sample sizes were too small in other years.

Recovery rates for adult males, young males, and young females were significantly higher ($P = 0.01$, $P = 0.02$, and $P = 0.09$, respectively) in the Eastern reference area. Recovery rates for adult females were not different between the two regions. A composite Z test showed a significantly ($P < 0.001$) higher overall recovery rate for the Eastern area.

We also tested the null hypothesis that survival rates were similar for woodcock from the two areas. The null hypothesis could not be rejected for any age-sex class (Table 5). Approximate powers (corresponding to a true survival rate difference of 0.10 and $\alpha = 0.10$) were extremely low, ranging only from 0.14 to 0.16. In all four age-sex classes, the mean survival rate estimate was lower for Eastern woodcock than that for Central birds (Table 5). For all classes except young females, the difference was substantial. A composite test statistic over all age-sex classes approached significance ($Z = -1.56$, $P = 0.12$). The lack of precision of our survival estimates and the resulting low power of our hypothesis tests hampered our ability to investigate possible geographic variation in survival rates. Our results, however, lead us to suspect that survival rates of woodcock in the Eastern unit are lower than those of birds in the Central unit.

Regional comparisons of recovery rates often permit inferences about comparative harvest rates. Our analysis indicates that recovery probabilities for birds from the Moosehorn National Wildlife Refuge differ from those for the rest of the Eastern unit. Although this heterogeneity of recovery rates does not bias survival estimates or create problems with recovery rate tests within reference areas, it does result in misleading comparisons between recovery rates for the reference areas. After eliminating Moosehorn bandings, the evidence is quite strong, for a small sample of years, that Eastern reference area birds are harvested at a higher rate than Central area birds (if reporting rates and survival from banding until the hunting season are equal between the areas). The comparison of regional survival rates provided some indication that overall survival rates

Table 5. *Results of testing hypotheses regarding differences in woodcock recovery and survival rates between the Eastern and Central reference areas.*

		Recovery rates[a]			Survival rates[b]		
Age–sex class	Years	$\bar{f}_E - \bar{f}_C$	Z	P	$\bar{S}_E - \bar{S}_C$	Z	P
Adult M	1969-75	0.011	1.16	0.25	-0.135	-0.79	0.43
Young M	1969-75	0.005	0.78	0.43	-0.184	-1.20	0.23
Adult F	1969-74	0.000	-0.04	0.97	-0.153	-0.95	0.34
Young F	1969-74	0.006	0.60	0.54	-0.028	-0.18	0.85

[a] Results of a z test (Brownie et al. 1978:180-182) testing the null hypothesis that recovery rates of Central and Eastern woodcock were similar. The difference between mean annual recovery rates for the two areas is denoted by $\bar{f}_E - \bar{f}_C$.

[b] Results of a z test (Brownie et al. 1978:180-182) testing the null hypothesis that survival rates of Central and Eastern woodcock were similar. The difference between mean annual survival rates for the two areas is denoted by $\bar{S}_E - \bar{S}_C$.

may be lower for Eastern unit birds. We have no evidence about what factors (hunting or nonhunting) might be responsible for this difference.

Temporal Variation

We were interested in learning whether survival and recovery rates varied over time or remained constant from year to year. We first used a 2 × n chi-square test to test the null hypothesis that direct (first hunting season after banding) recovery rates were constant from year to year. This hypothesis was not rejected ($P > 0.10$) for any of the adult data sets, and a composite test statistic for all adults (obtained by summing chi-squares and associated degrees of freedom) was also nonsignificant ($P > 0.10$). However, three of the four data sets for young birds showed significant ($P < 0.05$) temporal variation (Table 6). The hypothesis tests for young birds were much more powerful than those for adults because of the substantially larger sample sizes.

Temporal variation in survival rates was examined by means of the likelihood ratio test of models H_{02} vs. H_1 (Brownie et al. 1978:87). Specifically, we tested the hypothesis that recovery rates vary temporally but that survival rates are constant versus the hypothesis that both survival and recovery rates vary temporally. Although the test statistics for males were nonsignificant (Table 6), those for Eastern females were significant ($P < 0.10$), and those for Central females approached significance ($P = 0.11$). Thus, there is some evidence of temporal variation in survival rates for females, but not for males.

Population Model

A knowledge of survival rates alone does not permit inferences to be made about rates of population change. Such inferences also require information on reproductive or production rates. We attempted to obtain crude estimates of production by using a method commonly employed in continent-level studies of migratory bird populations (see Martin et al. 1979:207). This method involves estimating the age ratio in a sample (our sample consisted of wings provided by hunters) and the differential probability of being sampled (estimated as the ratio of recovery rates of young to adult banded birds), and then "correcting" the sample ratio by the differential sampling probability.

Because of the discrete nature of the Eastern and Central woodcock populations of North America (Coon et al. 1977), we assumed that all woodcock produced in the Eastern reference area were harvested in the Eastern harvest unit and that all birds from the Central reference area were harvested in the Central harvest unit. We also assumed that the characteristics (particularly age structure and differences in age-specific recovery probability) of birds from the two banding reference areas were representative of all the birds from which the wing samples from the Eastern and Central harvest units were derived. Although this assumption is probably not strictly true, we believe it is reasonable for our purposes.

The age ratios (we used young/adult female) in the harvest were obtained from unweighted wing

Table 6. *Results of testing hypotheses regarding temporal variation in woodcock recovery and survival rates.*

Reference area	Sex	Years	Recovery rates[a] Adults df	X^2	P	Young df	X^2	P	Survival rates (young and adult)[b] df	X^2	P
Eastern	M	1967–75	8	11.72	0.16	8	11.07	0.20	15	7.83	0.93
	F	1967–74	7	2.83	0.90	7	15.06**	0.04	13	21.47*	0.06
Central	M	1969–77	8	11.10	0.20	8	45.59***	0.00	14	13.34	0.50
	F	1969–77	8	6.75	0.56	8	28.16***	0.00	14	20.76	0.1

[a] Results of 2 × n contingency tests of the null hypothesis that direct (first-year) recovery rates were constant from year to year.

[b] Results of likelihood ratio tests of model H_{02} vs. H_1 (Brownie et al. 1978:87), testing the hypothesis that recovery rates varied temporally but that survival rates were constant versus the hypothesis that both survival and recovery rates varied temporally.

*$0.05 < P < 0.10$.

**$0.01 < P < 0.05$.

***$P < 0.01$.

survey data published in the woodcock status reports (e.g., Artmann 1977:Table 5). We computed harvest age ratios for each of the two harvest units. Estimates of differential vulnerability were then obtained as the ratio of young to adult female recovery rates (Tables 1 and 2) for the two banding reference areas. The harvest age ratios were then divided by the differential vulnerability ratios, and production rates were estimated.

Because of the variability of the data, we computed production rates in two different ways as a check on consistency. One procedure involved computing annual production rate estimates using annual estimates of harvest age ratio and differential vulnerability, and then computing a mean production rate from the annual estimates. The other procedure involved direct computation of a production rate estimate, using mean estimates of harvest age ratio and differential vulnerability. Although these two computational methods yielded estimates which differed (although not greatly), the Eastern estimate was consistently lower than that for the Central area. We have already noted that some of the assumptions required in our estimation methodology were not strictly met. In addition, both ratios required in our procedure (harvest survey wing age ratios and recovery rates of banded birds) were estimated and contain sampling variation.

Despite our uncertainty about the accuracy of the production rate estimates, we chose to use them in conjunction with our survival rate estimates in a simple modeling effort. We used a population projection matrix (see Martin et al. 1979:215–218) which assumed constant survival and production rates over time and a sex ratio of young birds in both populations of 50% males. Asymptotic rates of population increase (ratios of population size in successive years) computed with the model were 1.2 to 1.3 times higher for the Central area, depending upon which production rate estimates were used. This result should be viewed with some caution because of the assumptions required (e.g., constant production rates) and because of the considerable sampling variation associated with the survival and production rate estimates. Nevertheless, our modeling results are consistent with evidence provided by other authors that there are important differences between Eastern and Central woodcock populations. For example, singing-ground surveys conducted in the two regions (Artmann 1977; Tautin, personal communication) show different trends, with the Eastern unit breeding population index showing a consistent decline over the past 10 years. Also, Krohn et al. (1974) expressed concern over the low survival rates of a large group of woodcock banded in Maine.

Conclusions

Results of our analysis indicate that survival rates of Eastern woodcock are lower but that recovery rates are higher than those of Central woodcock. Annual production rate estimates were also lower for Eastern unit woodcock, and our simple modeling effort indicates differences in rates of population growth for the two regions. Although our production rate data and population projections are subject to many potential biases, there nevertheless may be some cause for concern for the Eastern population of woodcock.

Woodcock population dynamics in general are unlike those of other migratory game birds that have been subjected to intensive study. Unlike most waterfowl species, female woodcock exhibit higher survivorship than males, and there apears to be no age-specific difference in vulnerability to shooting. Woodcock, especially young males, show quite high annual mortality rates. This species characteristic may prove to be the most important in determining overall population structure. Because of these differences in population dynamics, we suggest that caution should be used in applying principles and concepts developed for waterfowl to the management of woodcock populations.

Recovery rate estimates for woodcock seem to indicate that hunting mortality comprises a small amount of the total annual mortality. If band reporting rates for woodcock are quite low, however, the apparent low recovery rates for this species may be misleading. Estimates of crippling loss must also be applied to estimates of harvest rates to obtain true kill rates. Pursglove (1975) indicated that crippling loss could be as high as 17%. Without reliable estimates of band-reporting rates and crippling loss, the relative importance of hunting and nonhunting mortality to American woodcock cannot be accurately ascertained. Also, we note that even if the kill rate could be estimated, a knowledge of its magnitude would not permit inferences to be made about the effects of hunting on woodcock populations.

We did not attempt to examine woodcock banding data for the effects of hunting on survival rates, as has been done for the mallard (*Anas platyrhynchos*) by Anderson and Burnham (1976) and Rogers et al. (1979) and for the canvasback (*Aythya valisineria*) by Nichols and Haramis (1980). Woodcock hunting regulations have remained virtually unchanged during the period covered in our analysis, and the large sampling errors associated with our estimates would probably result in tests of extremely low power.

Woodcock, especially adults, are difficult to band in sufficient numbers to obtain precise estimates of survival or recovery rates. Yet the popularity of woodcock as a hunted species and our best estimates of overall harvest have been steadily increasing (Martin 1979). An adequate sampling frame of woodcock hunters would enable an accurate assessment of the actual harvest and would provide information that could be used to obtain better production rate estimates. However, even the information provided by a harvest survey would not, by itself, be sufficient to provide an adequate measure of population status. Such a goal would require estimates either of population size or of both survival and production rates.

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Age Determination of American Woodcock Chicks by Bill Length

by

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Abstract

A formula for age determination for chicks of American woodcock (*Philohela minor*) has been in general use by investigators of woodcock breeding biology since 1967. A critical assessment of this technique was made, using additional data from 184 examinations of 127 chicks with known hatching dates. Regression techniques confirm the accuracy of this rule-of-thumb formula (age in days = bill length in millimeters - 14 ÷ 2) for use with chicks until they reach 15 days of age. Additional data from at least two examinations of 191 chicks whose age was not known support this conclusion, as well as furnishing a key (albeit less reliable) to aging chicks from 15 to 35 days of age. Records from a few sexed chicks indicated that the differential growth rates of males and females do not introduce any serious error in age estimation until at least 15 days of age.

Hatching dates provide essential data on woodcock breeding biology, but they are difficult to obtain. Probably the most productive source of such information is broods located with pointing dogs, a technique first used by Gus Swanson in 1937 (Mendall and Aldous 1943:140). The rapidly growing bills of chicks provide a practical means of calculating their ages with acceptable accuracy. Pettingill (1936:324–326) was probably the first to measure the bill length of American woodcock chicks at hatching and in several growth stages; his work gave me the idea of using the technique to derive hatching dates.

Previously I described a rule-of-thumb method for calculating hatching dates of woodcock chicks (Ammann 1967). The formula was derived from bill measurements of chicks whose hatching time was known to within 12 h and from bill measurements of some of the same chicks that had been recaptured one or more times; a graph of these measurements was included to illustrate the rate of growth. My primary purpose at that time was to determine hatching peaks in various regions of Michigan to facilitate efforts by cooperators searching for broods with pointing dogs. In a later publication describing brood capture techniques (that also summarized and evaluated some of the results), I again mentioned the chick-aging method and illustrated it with a growth curve based on additional data (Ammann 1973).

The objective of the present study was to reexamine this aging technique on the basis of more recent information from Michigan and from several other states. In particular, more data are now available on older, flying chicks, including some that have been sexed.

Data Source

Measurements of chick bill lengths were obtained from broods found by game biologists or their assistants, under close supervision. For 20 years I have searched for broods with pointing dogs, at first on a modest scale as part of (or in addition to) my work as a game bird specialist with the Michigan Department of Natural Resources. After retiring in 1974, I was able to intensify this activity (not only in Michigan but also in several other states, chiefly Alabama, North Carolina, West Virginia, Missouri, and Maine) and worked in cooperation with State or Federally funded woodcock investigators. In this paper, however, I have not included data from the southern states because of the possibility that the growth rates there differ from those of northern woodcock.

Except in a few instances, my co-workers and I did not attempt to capture the same broods repeatedly. However, a number of broods were located again, and a few were found several more times, either by chance or with the express objective of capturing hens or chicks that had been missed in the first search.

Nests found during brood searches were checked frequently to increase the chance of finding the broods as soon as possible after hatching. Even so, it was seldom possible to determine to the hour when the chicks hatched because the hen normally broods chicks throughout both the hatching and drying-off period (probably several hours). The hen almost certainly then would lead the chicks away from the nest, within 1 or 2 h. The presence of an egg tooth on one or more of the chicks was taken to indicate a very recent hatch.

I defined a "known-age" chick as one that was known to have hatched no more than 12 h before capture. Bill measurements of chicks captured within a few hours of hatching, and subsequent measurements, are the basis of the aging method described here. Ages of chicks at recapture were calculated to the nearest day.

Two measurements or more were obtained for many additional chicks in all growth stages (from downy young to fully grown juveniles) whose hatching dates were unknown. These additional data were valuable when used in conjunction with the known-age data. The intervals between any two measurements for this group of chicks was also calculated to the nearest day.

Growing chicks, 12 days or older, were sexed by outer primary width (Blankenship 1957: 89–98). This method is not entirely reliable and is subject to the same error as that for fully grown woodcock sexed only by the primaries. Some chicks of unknown age were also collected and sexed by dissection. When chicks were recaptured in summer or fall as full-grown juveniles, they were sexed externally. The most reliable data were provided by dissection or by external sexing of juveniles.

The exposed culmen (from the anterior end of the bill to the posterior end of the "V" on the exposed portion of the upper mandible) was measured to the nearest 0.5 mm with calipers or with a millimeter rule. Because all chicks were banded when first captured, they could be positively identified at recapture.

Table 1. *Examinations of known-age woodcock chicks performed in the first 15 days after hatching.*

	Number of	
Examination frequency	Chicks	Examinations
At hatching only	76	76
At hatching and one or more times thereafter	32	88
Only after hatching, one or more times	19	20
Totals	127	184

Known-Age Chicks

Hatching dates were determined for 38 broods. Of these broods, 6 were not located until several days after hatching and 21 were never contacted again after they were discovered at hatching. Some of the 127 known-age chicks were examined more than once (total, 184 examinations; Table 1).

Bill Length At Hatching

At hatching, the mean bill length of 108 chicks (in 32 broods) was 14.32 mm (range 10 to 16 mm), with 95% confidence limits of ± 0.19. Two chicks in different broods, with bill lengths of 10 and 11 mm, appeared to be distinctly smaller than their broodmates and probably should be regarded as abnormal, or runts; such occurrences are rare. In all of the other broods, bill lengths seemed quite uniform among chicks of each brood. In 15 broods of 4 chicks each, only 5 had a spread of 1.5 mm or more between the longest and shortest bill. With such small measurements under often difficult field conditions, some measurement error must be expected, although it probably was not significant for the purposes of the present study. In comparison, Pettingill (1936) examined 20 newly hatched chicks and reported bill lengths averaging 14.7 mm (range, 13 to 19.5 mm).

Bill Growth After Hatching

The bill measurements of all the known-age chicks were studied by linear regression techniques. A linear equation was calculated from

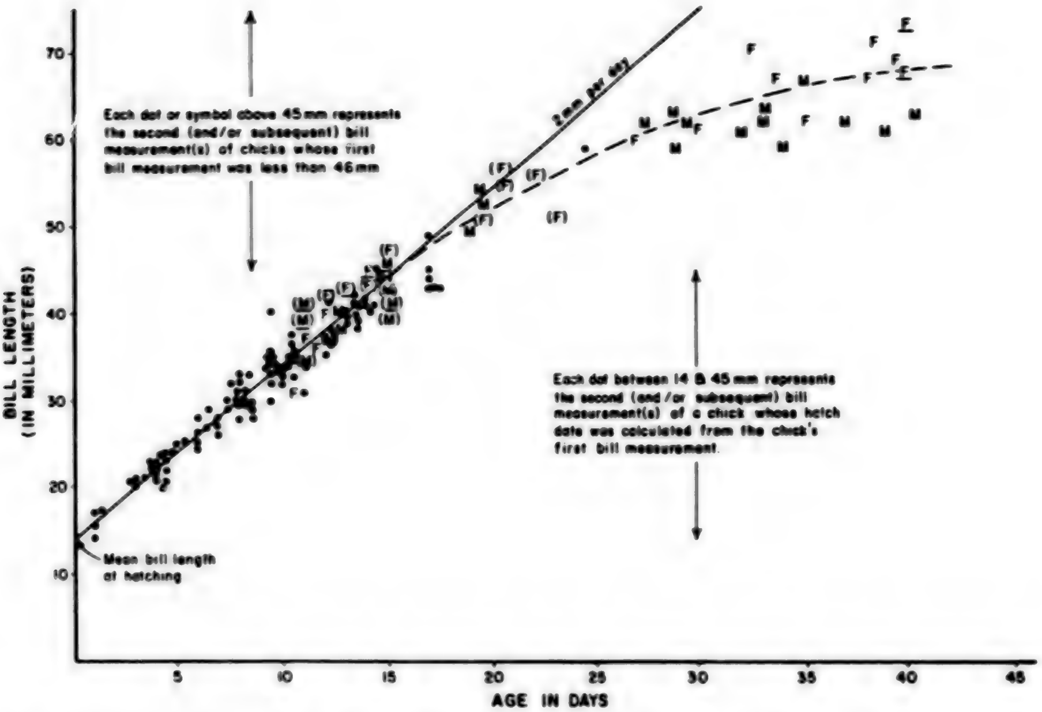

Fig. 1. Growth of woodcock bills. Dots indicate chicks of unknown age. Symbols for sexed and known-age chicks are M or F = sexed by dissection or when captured as full-grown juvenile and (M) or (F) = sexed as a chick by outer primaries only; underlined symbols = sexed known-age chicks.

these data to predict age as a function of bill length. The resulting equation is $\hat{Y} = 0.4808 X - 6.769$, where $\hat{Y}$ is the predicted age in days and X is the measured bill length. One can calculate from the equation that a change of 2.0799 mm in measured bill length (X) corresponds to a 1-day change in predicted age ($\hat{Y}$), which is in close agreement with the previous rule-of-thumb formula (age in days = bill length in millimeters − 14 ÷ 2, where 14 represents bill length at hatching and 2 the growth in millimeters per day).

Unknown-Age Chicks

Two or more bill measurements were obtained from 191 chicks whose hatching dates were unknown and whose bills were 45 mm or less. All of the chicks in each brood were aged the first time they were captured by applying the rule-of-thumb formula to the average bill length of the chicks in the brood. From capture dates I then calculated the presumed age of each chick when it was recaptured. A plot of some recapture data (Fig. 1) enables evaluation of bill growth with reference to a constant increase of 2 mm/day (solid line). The dots indicate chicks of unknown sex; chicks that were sexed and a few whose age also was known are represented by symbols. The digression of the dots and symbols from the straight line indicates how closely these data for chicks of unknown age agree with those for known-age chicks, and further validates the aging formula for chicks to at least 15 days of age.

After about 15 days, the growth rate apparently decreases gradually until 40 to 45 days, when the bills are essentially fully grown. However, after 15 days of age, chicks flush more readily and very few are captured by brood searching. The few older chicks that are captured can be aged approximately by referring to the curved, broken line in Fig. 1, until their bills approach full growth at about 60 mm. For example, a 55-mm bill would indicate a chick about 24 days old.

Sex Bias in Aging Chicks

Because adult female woodcock have longer bills than adult males, we should expect this sex difference to show up at some time during the chick's growth. It's possible, therefore, that a differential growth of the sexes might result in a bias when chicks are aged by the bill-length method. Inspection of Fig. 1, however, does not indicate a distinct tendency for the bill length of female chicks to exceed that of males until possibly at or after about 35 days. More data might show an earlier divergence.

A different approach might be to compare bill lengths of chicks of both sexes occurring in the same brood, if all could be examined at the same time (chicks in a brood hatch almost simultaneously). A cursory examination of chicks in 17 broods ranging from 3 to 14 days old (estimated), each of which contained chicks of both sexes, showed no consistent tendency toward longer bills in the females. Although the female chicks had apparently outgrown their male broodmates by 1 to 7 mm (X = 3 mm) in 7 of the 8 of these broods that were about 12 to 14 days old, only 10 chicks of each sex were involved. All were sexed by the outer primaries alone, and the validity of these data is thus open to question. It appears, however, that we need not be concerned about errors in aging chicks up to at least 15 days on the basis of differential bill growth of the sexes, especially if the average bill measurement for all the chicks in a brood is used for the computation. However, hens occasionally adopt chicks from other broods, and any chick whose bill length differs markedly from that of its broodmates should be viewed with suspicion. An adopted chick that is not the same age as its companions can usually be detected by comparing its plumage development, if not its size, with that of the other chicks.

Conclusions

A reassessment of the rule-of-thumb formula (age in days = bill length in millimeters − 14 ÷ 2) by linear regression techniques indicated that it is satisfactory for aging woodcock chicks captured by the brood-search method. Approximate ages of older, flying chicks can be obtained from the growth curve shown in Fig. 1.

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A Revised Technique for the Identification of Individual Woodcock

by

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Abstract

The purpose of this study was to determine the usefulness of color banding for the identification of individual woodcock. Reflective color bands were placed on 302 birds captured at singing grounds and/or summer fields. These marked birds were subsequently shined with an aircraft landing light to ascertain the color and position of the bands. Over 500 observations made during a two-year period resulted in a successful identification rate of 86%. The mean distance at which birds were identified was 15.2 m (range = 3.05 to 62.5 m). Woodcock showed little to no abberant behavior as a result of being spotted.

Several researchers have pursued various methods for marking and subsequently identifying individual woodcock (*Philohela minor* Gmelin)(Ramakka 1972; Beightol and Samuel 1973). If successful, such techniques would be instrumental in studying behavior on singing grounds and in mark-recapture efforts to estimate populations.

The use of sonagrams for the identification of individual woodcock has been the subject of several studies (Beightol and Samuel 1973; Courture and Bourgeois 1974). Findings from these studies, however, have been contradictory and inconclusive. Ramakka (1972) stated that radio packs placed on displaying male woodcock severely reduced courtship activities and caused atypical breeding behavior. Plastic neck markers used by Westfall and Weeden (1956) appeared to be effective for several weeks. The authors, however, did not discuss the possibility of increased predation or tag visibility at night. Richter and Liscinsky (1955) used leg bands covered with reflective sheeting to mark birds. They identified individuals by illuminating the color bands in the beam of a five-celled flashlight. This study attempted to improve the reflective leg-band technique by using a brighter, more concentrated light source and more efficient reflective materials.

Study Area and Methods

This study was conducted at McClintic Wildlife Station, 11 km north of Point Pleasant in Mason County, West Virginia. The area is bounded on the west by the Ohio River and on the east by a semicircular ridge system. This state-owned facility of 1,012 ha is characterized by abandoned croplands with actively cultivated areas interspersed. Second-growth forests, open fields, and brushy regions are present in equal proportions on the area (Major 1973; Waggy 1973; Bickerton 1979).

Woodcock were captured on singing grounds and summer fields by using mist nets (Sheldon 1967), nightlighting (Rieffenberger and Kletzly 1967), and a modified nightlighting technique (B. P. Shissler 1980). A single U.S. Fish and Wildlife Service band and one to three reflective color bands were placed on each bird. These color bands consisted of unnumbered 3-A aluminum alloy bands (National Band and Tag Co., Newport, KY 41072) covered with Scotchlite reflective sheeting (3M Corporation, 3M Center, St. Paul, MN 55101). The Scotchlite has a pressure-sensitive adhesive coating.

Band position (e.g., right or left leg, both legs, or two on the same leg) plus different color combinations were used to distinguish individual woodcock. The colors used were red, green, yellow, gold, blue, and black, allowing 552 leg positions/color combinations. All females received a single blue band. Each color band weighed approximately 0.4 g.

A spotlight fashioned from an aircraft landing light was used to illuminate the birds (Rieffenberger and Kletzly 1967) (Fig. 1). Woodcock displaying on singing grounds were approached while they were airborne. The distance from which the bird was illuminated was determined by the observer, who considered intervening vegetation, band visibility, bird disposition, and time available. Birds were spotted both on the ground and in the air.

Singing grounds were revisited every four days, and displaying woodcock were illuminated. Summer fields were nightlighted once each week from 18 May to 15 August 1979. Identification distances were estimated in 1979, but marked and measured in 1980.

Results

Positive identifications were made in 83.9% of 432 attempts at singing grounds (Table 1). Partial identifications were made in 9.8% of the observations. The mean estimated spotting distance was 18.0 m (range = 4.50 to 61.0 m) and 15.2 m (range = 3.05 to 62.5 m) for measured distances.

Fig. 1. Illuminated woodcock, showing reflective color band.

Examples of the type of data generated by this technique are as follows. A minimum of 19 singing grounds had the same occupants for 41 to 71 days. In addition, nondisplaying males were identified on singing grounds by their color bands on at least 15 occasions. Movements between singing grounds by displaying males were noted on 48 instances.

On summer fields, 103 birds were caught and color banded. In addition to those captures, 164 woodcock were encountered while nightlighting. Of these, 42.1% were color banded. Successful identification was made on 88.5% of 69 attempted spottings.

The reaction of displaying males to being illuminated varied among individuals. Forty-five percent continued to peent and "behave normally," 10.6% became momentarily silent or walked a short distance, 37.2% went into display flights but returned to their original landing site, and 7.1% temporarily deserted the immediate display area. Observations indicated that no bird deserted a singing ground as a result of being spotted.

Color bands were recovered (n = 16) from woodcock harvested during the fall of 1979, and from returning males in the spring of 1980. Mean tag recovery time was 274 days (range = 62 to 417 days). None of these bands had any tape loss, and when shined side by side with new color

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Table 1. *Degree of identification success of woodcock on singing grounds.*

Year and observers	Number observations	Number of identifications (% in parentheses) Successful	Partial	Failure	Average distance (m)
1979[a]					
1	74	63 (93.2)	3 (4.1)	2 (2.7)	16.7
2	72	65 (90.2)	3 (4.2)	4 (5.6)	19.3
3	36	N.D.	N.D.	N.D.	N.D.
Others	19	N.D.	N.D.	N.D.	N.D.
Total	201	134 (91.8)	6 (4.1)	6 (4.1)	18.0
1980					
1	82	68 (83.0)	7 (8.5)	7 (8.5)	11.7
2	86	59 (68.6)	19 (22.1)	8 (9.3)	20.8
3	34	30 (88.4)	3 (8.8)	1 (2.8)	N.D.
4	29	25 (86.2)	2 (6.9)	2 (6.9)	13.0
Total	231	182 (78.8)	31 (13.4)	18 (7.8)	15.2
Grand total	432	316 (83.9)	37 (9.82)	24 (6.37)	

[a] Observer 3 and those designated "others" returned no data on percent success or failure as only successful attempts were recorded.

bands, no difference in reflective qualities could be detected. When compared in natural light, they appeared slightly faded.

Discussion

Color banding was found to be an effective and inexpensive field technique for identifying individual woodcock. When illuminated, bands were readily visible during twilight and nighttime hours. Observers were able to identify individual birds by the position and color of the bands. Successful identifications were made in the air as well as on the ground.

Most visible and easily distinguished were the bands using red, yellow, or green sheeting. Blue and black were not readily visible and were easily confused with other colors. Color qualities of gold and yellow were so similar that no distinction could be made in the field. Single bands of more than one color could not be identified at distances greater than 4 m and therefore were not used. The possibility of using a spotlight mounted on binoculars or of using two-man teams (one to direct the light and one to identify the bird) may increase the effectiveness of the technique.

The 3M Corporation also produces a High Intensity Scotchlite sheeting in nine colors, which is reported to have 2.5 times the brightness of the engineering sheeting used in this study.

Management Implications

The effectiveness of color banding enables researchers to monitor woodcock activities with a minimum amount of disturbance. This may be of particular importance in some studies associated with singing grounds. Areas for application could include: male fidelity to singing grounds, movements between display areas, differences between male and female behavior, and breeding relationships between migrant and resident woodcock. Information in these areas would be valuable in reevaluating present methods of interpreting annual population surveys or indices.

On summer fields, woodcock could be identified as marked or unmarked without being captured. These birds could be specifically identified as members of a banded subpopulation. These subdivisions might include birds banded during different time periods (e.g., different colors or combinations each week), simple numerical groups (e.g., every 10 birds), or different age and sex categories (e.g., adult male, immature female). The ability to categorize birds without recapture could result in sample sizes large enough to allow reasonable population estimates. Statistical models similar to the Schnabel (1938) method could be designed to make use of successive samplings composed of known numbers of marked and unmarked individuals. The marked group could further be subdivided into the aforementioned subpopulations. By using this method, a re[illegible] estimate of recruitment from one year to the [illegible]t could be made.

Currently, a most pressing need in woodcock management is to determine the relationship between singing-ground censuses, yearly recruitment, and subsequent fall populations. Color banding provides a technique to help answer this important question.

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Woodcock Singing-Ground Counts and Breeding Habitat

by

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Abstract

A comparison of woodcock (*Philohela minor*) singing-ground counts, number of nesting hens, and available habitat in northern Wisconsin indicated a strong relationship. The singing-ground survey provides valuable information on relative breeding densities and population trends and may be the best indicator of breeding habitat trends.

An evaluation of several methods of censusing woodcock in Maine during the late 1930's resulted in the recommendation of a yearly count of occupied singing grounds as the most promising technique (Mendall and Aldous 1943). Organization of such counts into a systematic survey began in the early 1940's, and the present singing-ground survey is used as an annual index of the size of the breeding population. Since the singing-ground survey was begun, it has been evaluated and refined (Sheldon 1953; Kozicky et al. 1954; Goudy 1960; Duke 1966), with resulting improvements, notably in the random selection of route locations.

Studies of woodcock breeding behavior have disclosed the existence of a significant number of nonterritorial or subdominant males (Sheldon 1967; Godfrey 1974). If the ratio of territorial to nonterritorial males changes from year to year or differs between geographic areas, results of the survey would not accurately depict population trends. Thus, although about 1,000 woodcock routes are now conducted each spring (Tautin 1977), doubts remain about the validity of the survey. Because the survey involves a substantial amount of effort each year, it is important that such uncertainties be resolved.

Godfrey (1975) suggested the survey could be improved by counting the number of males per singing ground. Determination of this ratio, however, would require that observers possess a relatively sophisticated knowledge of woodcock breeding behavior. Couture and Bourgeois (1977) proposed another method of improving the survey that involved duplicate counts of individual routes. Since these suggested revisions would add to the survey costs, it is unlikely that either method would be adopted at a time when all roadside surveys are being scrutinized because of escalating energy costs.

Sheldon (1967) believed that singing-ground counts may be better indicators of habitat change than of population change. A significant relation was found between habitat cover classes and the number of singing males heard on New Brunswick woodcock routes (Dobell 1977). Furthermore, Ammann (1977) implied a strong relation between singing-ground counts and nesting habitat by his statement, "The more males in any one area, the better the chances for finding broods." In contrast, Couture and Bourgeois (1977) reported no relation between singing males and number of nesting females on their Quebec study area; the size of their study area was only 20 ha, however, which leads one to view their conclusion with some skepticism.

The objectives of the present study were (1) to determine the density of active woodcock singing grounds in typical forested habitats in northern Wisconsin and (2) to determine the correlation between singing-ground counts, number of nesting hens, and available habitat.

Study Area and Methods

The study was conducted in the Hoffman Lake–Hay Creek Wildlife Area and an adjacent portion of the Chequamegon National Forest about 15 km northeast of Park Falls, Wisconsin.

Soil types vary considerably within the study area but generally consist of sands or sandy loams on the uplands and peat in the lowlands. Several streams, lakes, and marshes are interspersed throughout the area. The land area is more than 90% forested; in order of abundance, aspen (*Populus* spp.), swamp conifers, fir-spruce (*Abies balsamea* and *Picea* spp.), and northern hardwoods are the most important forest types.

Singing male woodcock were censused each spring during 1977–80 along 29 km of roadway circumscribing the study area; the census transect was divided into 18 segments, each 1.6 km long. Transect width was established as 400 m, on the basis of an estimated 200-m hearing distance for singing males. Censusing was done during both morning and evening performance periods, with up to 12 cooperators involved on some days. Censusing was carried out on foot, with each cooperator working a single segment during any one session. Only singing grounds that were occupied on two or more occasions were included in the total.

Nest searches were conducted each spring in the area censused for singing males. All searching effort was recorded and tallied by the census segment (1–18) in which it occurred. The searching crew generally consisted of two men and one or two bird dogs, except in 1978 when several high school classes assisted in the nest search. Artificial woodcock nests (small wooden blocks) were set out to provide a measure of the searching efficiency of student groups. Insufficient manpower was available to search the entire census area, so the coverts that appeared most attractive were searched first. Relatively little time was thus spent searching habitats (such as northern hardwoods or conifer plantations) that lacked the shrub components preferred by nesting woodcock hens (Gregg and Hale 1977).

Experience gained during trapping and telemetry work revealed that brushy habitats, especially alder (*Alnus* spp.) and young aspen, comprise the major portion of preferred woodcock habitat in this locale. Therefore, the amount of area occupied by aspen, upland brush (including small grassy openings), and lowland brush were tallied for each of the 18 census segments and served as a measure of available habitat. The amount of habitat was then compared to the number of singing males and nests found within each segment to determine the correlation between breeding birds and habitat.

Singing-Ground Census

Application of the 200-m hearing range for singing male woodcock to the length of the transect resulted in a census area of nearly 1,160 ha. Singing-ground counts within that area were 56, 63, 66, and 58 during the 1977–80 period (Table 1). Three singing grounds located slightly more than 200 m from the road were included in these totals because the relative scarcity of grounds more than 150 m from the road indicated that a portion of the more distant singing grounds were being missed. The average right-angle distance from the center of the roadway was only 64 m for 44 singing grounds measured in 1979; only 9 of the 66 singing grounds located that spring were believed to be more than 150 m from the road.

The density of active singing grounds within the census area averaged 5.3/km^2. Sheldon (1967) estimated a similar singing-ground density of 5/km^2 for the entire Quabbin Reservation in Massachusetts. A lower density of 2/km^2 was reported by Godfrey (1974) for a 1,600-ha study area in Minnesota. Singing-ground densities of up to 10/km^2 have been reported (Norris et al. 1940; Mendall and Aldous 1943), but the higher densities were associated with smaller blocks of cover.

The total number of singing grounds within the census area remained relatively stable during the four years of the study, despite sizeable changes in singing-ground counts in some segments of the census area (Table 1). Year-to-year changes in singing-ground counts in segments were substantially less, however, than were the differences in counts between the best segment and the poorest. Average singing-ground counts among the various segments ranged from 0.75 to 7.5. Segments that contained small amounts of woodcock habitat generally evidenced very few singing males. Singing grounds were scarce, for example, in segments 6 and 11, where northern hardwood stands covered most of the area. When average singing-ground counts were compared with the amount of habitat available in each census block, a significant correlation ($r = 0.89$, d.f. = 16, $P < 0.01$) was found.

Although habitat quantity and singing-ground counts indicated a linear relation, habitat quality appeared to have a bearing on the strength of this relation. Woodcock prefer the early stages of forest succession, and habitat quality typically

Table 1. *The number of woodcock singing grounds and nests related to the amount of habitat in the Hay Creek study area, 1977–80.*

Census segment	Woodcock singing grounds					Total nests	Total man-hours	Nests per man-hour	Woodcock habitat (ha)[b]
	1977	1978	1979	1980	Mean				
1	2	0	1	0	0.75	1	10	0.10	14.6
2	4	2	3	0	2.25	1	20	0.05	20.2
3	2	3	4	4	3.25	3	20	0.15	17.8
4	2	4	4	3	3.25	0	3	–[a]	8.9
5	2	1	3	5	2.75	0	12	0.00	20.2
6	1	2	2	2	1.75	0	4	–	5.3
7	2	2	2	1	1.75	0	4	–	8.9
8	3	6	5	4	4.50	3	20	0.15	26.3
9	5	4	5	4	4.50	2	14	0.14	27.1
10	5	6	5	4	5.00	2	15	0.13	26.7
11	0	2	1	2	1.25	0	3	–	2.8
12	5	4	3	1	3.25	2	17	0.12	17.4
13	6	7	8	9	7.50	21	117	0.18	55.0
14	3	4	5	3	3.75	7	62	0.11	28.7
15	2	2	1	0	1.25	0	3	–	4.4
16	6	6	6	6	6.00	4	47	0.09	29.9
17	5	4	5	7	5.25	8	89	0.09	25.9
18	1	4	3	3	2.75	5	23	0.22	18.6
Totals	56	63	66	58		59	483	0.12	358.7

[a] Not calculated if searching time was less than 10 man-hours.

[b] Woodcock habitat was defined as the amount of area occupied by aspen, upland brush, and lowland brush within each census segment.

declines as forests mature. Most of the aspen stands in the Hay Creek Wildlife Area were young and therefore constituted woodcock habitat of high quality. The aspen stands in the Chequamegon National Forest portion of the study area were more mature, however, and received little use by singing males. Segments 1 and 2, for example, contained 10% of the woodcock habitat within the census belt but accounted for only 5% of the singing grounds.

Woodcock Nest Searches

Nest-hunting efforts during the four years of study resulted in 76 nests and 46 broods found during 795 man-hours of searching, but only 59 nests located by project personnel during 483 man-hours of searching were included in the present analysis (Table 1). Broods were excluded because their mobility made it impossible to be certain that they had been produced within the census block where they were found and to avoid the possibility of "recounting" nests. Nest searching efforts by high school groups were also excluded because the efficiency of students in finding nests was not comparable to that of experienced personnel. High school students found only 29% of the simulated woodcock nests used to gauge searching efficiency and discovered only 6 real nests during 267 man-hours of hunting.

Results of searching efforts among census blocks varied considerably, with totals ranging from 0 to 21 nests for the duration of the study (Table 1), but the amount of time spent searching within these census segments also varied because it depended on the quantity of potential nesting habitat within each segment. Relatively little time was spent searching unproductive habitats, so the number of nests found per man-hour in the various segments did not differ widely. Because searching effort was not uniform between segments, no statistical correlation between the number of nests and number of singing grounds was attempted. Nevertheless, the available evidence suggests that the number of singing grounds and the number of nesting hens in a given locale are closely related.

Woodcock Populations and Habitat

The results of the present study suggest a strong relation between woodcock singing-ground counts, the number of nesting hens, and available habitat. Study results further suggest that optimum woodcock breeding habitat exists only for a brief time during the span of forest succession. Continued growth of our forests will cause a progressive shrinkage of woodcock habitat, and evidence is available that such losses are occurring in Wisconsin. In 1956, seedling and sapling stands comprised the largest share of Wisconsin's commercial forestland area, but by 1968 poletimber stands had become the dominant size class. During the same period, most of the nonstocked area was lost through planting (Spencer and Thorne 1972).

Although evidence still does not guarantee that results of the singing-ground survey truly reflect annual fluctuations in the breeding woodcock population, the survey undoubtedly provides valuable information on relative breeding densities and population trends. In addition, the singing-ground survey may have unrecognized value as a data source on breeding habitat trends. Mortality factors (such as hunting and pesticides) appear to have relatively little influence on woodcock population trends at present. Although weather, disease, and other agents contribute to fluctuations in woodcock numbers, habitat will ultimately determine population size. Efforts are under way to improve our data base on woodcock habitat, but we neither know how much habitat is now available in the United States nor how land-use changes affect habitat (Cushwa et al. 1977). Until a reliable method of inventorying woodcock habitat becomes available, singing-ground counts appear to be our best indicator of breeding habitat trends.

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Discriminant Analysis of the Peent Call for Identification of Individual Male American Woodcock[1]

by

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Abstract

Peent calls of male American woodcock (*Philohela minor*) were recorded on 24 singing sites in Centre County, Pennsylvania. Nine measurements of frequency, duration, and pulse rate were used to characterize the peent call sonagrams. The feasibility of applying discriminant analysis of peent call sonagrams to identify individuals was examined by using the calls of four birds over 8 to 11 display periods. The analysis correctly assigned 82% of the peent calls to the proper bird. The usefulness of sonagraphic analysis of woodcock peent calls for identifying large numbers of individual woodcock is limited by the high degree of overlap among the calls. However, the technique could be used effectively in studying the turnover of males on a small number of singing sites, particularly if the calls were examined in conjunction with behavioral cues.

Sonagraphic analysis of the peent call appears to be a feasible alternative to other methods for studying territoriality among male American woodcock (*Philohela minor*). Although the technique has been used successfully to distinguish among the peent calls of individuals of known identity (Beightol and Samuel 1973; Bourgeois and Couture 1977) and, in one instance, to examine the variation among the peent calls for three individuals over the course of the breeding season (Bourgeois and Couture 1977), no attempt has been made to use it in the recognition of a reasonably large number of unidentified individuals in a local population over the course of the breeding season. The purpose of the present study was to characterize the woodcock peent call, to investigate the differences among calls from different sites, and to determine the usefulness of sonagraphic analysis as a technique for identifying individuals without the necessity of capturing and marking.

Methods

We selected 24 woodcock singing sites in Centre County, Pennsylvania, for the study. Singing sites selected for recording were those for which behavioral cues strongly suggested that a single individual used each site during the recording periods.

Tape recordings of the peent calls from each site were made during dawn and dusk display periods from 12 March through 19 May 1977. From three to six singing sites were monitored during each display period, and recordings of 20 to 30 peent calls were obtained at each site.

The recording system consisted of a battery-operated Nagra 4.2 full-track tape recorder (Kudeleski S.A., Cheseaux/Lausanne, Switzerland) equipped with an electret-condenser highly directional microphone (Sennheiser Electronic Co., New York, New York) and foam windshield. The signal-to-noise ratio of the Nagra 4.2 is 88 dB, and its frequency response at 19 cm/s is 20 to 12,000 Hz.

Spectrographic (sonagraphic) analyses of the peent call were performed with a Kay Elemetric Company, Pine Brook, New Jersey, sonagraph (model 7029A) coupled with a sonagraph contour display unit (model 6070A) and amplitude display scale magnifier (Model 6076C). The contour display unit modifies the conventional sonagram to produce contour lines at 6-dB intervals.

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The scale magnifier was used to eliminate the upper 60% and lower 5% of the frequency range (160 to 16,000 Hz) and to magnify the remaining 35% (800 to 6,400 Hz). Use of these two techniques enables more accurate delimitation of the contour of the frequency bands, thereby reducing both subjectivity and error in time and frequency measurements. Recorded peent calls were transferred to the sonagraph magnetic plate at half the recorded speed.

The "correlation" procedure of the Statistical Analysis System (Barr et al. 1979) was used to compute the Pearson product-moment correlation coefficients between variables. The SAS "general linear model" procedure was used to perform univariate and multivariate analyses of variance. The SAS "Duncan" procedure was used to perform Duncan's multiple-range test for significant differences among the means of variables. The "discriminant" subprogram of the Statistical Package for the Social Sciences (Nie et al. 1975) was used to differentiate among calls of birds on different singing sites.

Results

Visual Inspection of Sonagrams

As expected, visual comparisons of peent-call sonagrams of several individuals recorded during single display periods disclosed that calls of a particular bird were similar in shape, duration, and frequency but generally different from those of other birds in one or more of these characteristics. Given a small number of birds and display periods, one can correctly assign many sonagrams to their respective birds by visual inspection alone (Beightol and Samuel 1973). However, when additional birds and display periods are included, the differences among sonagrams become less evident, and it becomes difficult, if not impossible, to correctly assign each peent call to the proper bird by visual inspection. The similarities in general features of the calls of the same bird and the apparent differences among birds nevertheless suggested that statistical analysis might permit identification of individuals by peent calls.

Measurements of Characteristic Features of Sonagrams

Seven bands were produced by contour display analyses (Fig. 1). We selected the very distinct second band (30-36 dB) to use in quantifying the woodcock peent call. The typical plateau shape of the peent call sonagram was used in characterizing the call: the frequency rises at the beginning of the call, remains at a constant frequency for approximately 150 ms, and then decreases at the end. Frequency and duration measurements of the three portions of the sonagram and the pulse rate were used to quantify the peent calls.

The following nine measurements were taken from the band at 30-36 dB of each sonagram (Fig. 1).

1. TD: total duration of band (ms).
2. PULSERT: pulse rate; calculated by determining the time period in which 10 pulses occur, beginning at 50 mm from the start of the band (ms).
3. F_1: frequency 1; initial frequency at center of band (Hz).
4. F_2: frequency 2; frequency at first point of inflection at center of band (Hz).
5. F_3: frequency 3; frequency at second point of inflection at center of band (Hz).
6. F_4: frequency 4; frequency at center of last pulse of band (Hz).
7. D_1: duration 1; duration of call from F_1 to F_2 (ms).
8. D_2: duration 2; duration of call from F_2 to F_3 (ms).
9. D_3: duration 3; duration of call from F_3 to F_4 (ms).

Correlations Among Measurements

As expected, none of the variables were independent, and high correlations were found between TD and D_2 measurements and among F_1, F_2, F_3, and F_4. These correlations introduced the possibility of using less than the full set of nine variables in studying variation in calls within and across singing bouts and singing sites.

Variation Among Peent Calls of a Single Bird

Peent calls were recorded during four display periods on one site from a bird that had been equipped by G. L. Storm with a small light-emitting device (Wolcott 1977). The amount of variation among calls recorded during different display periods relative to the variation among calls recorded during single display periods was calculated. When all nine variables were considered in

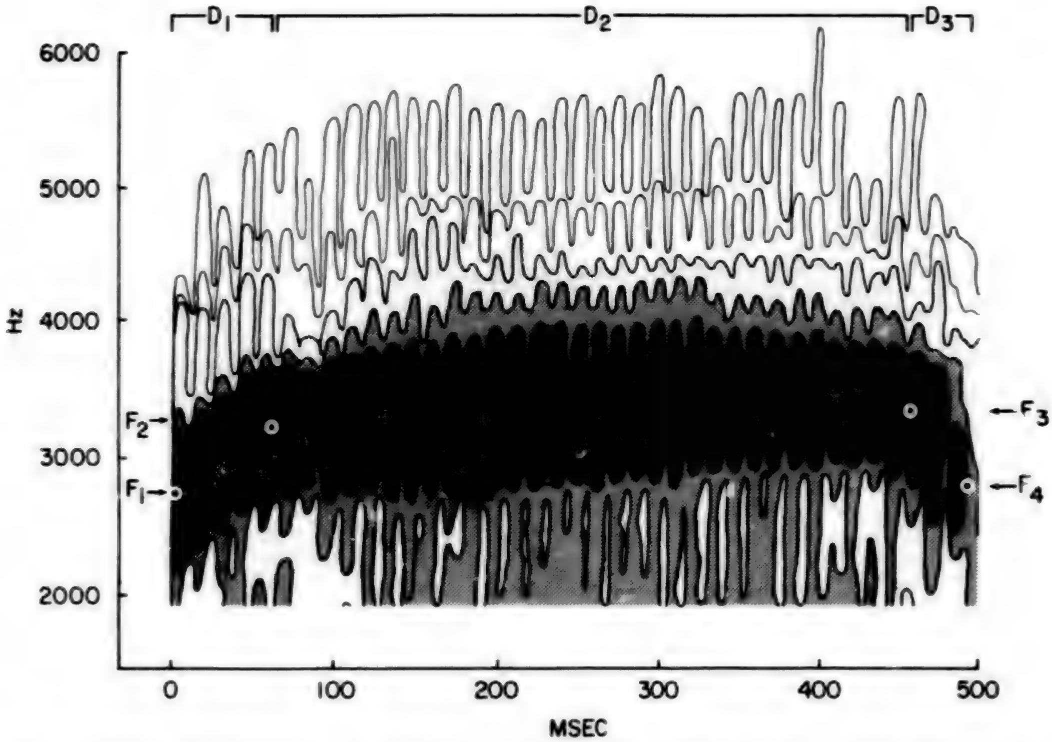

Fig. 1. Schematic representation of the American woodcock peent call, recorded at one-half normal speed onto the sonagraph magnetic plate. TD, total duration (ms) equals $D_1 + D_2 + D_3$; PULSERT, pulse rate (ms/10 pulses); F_1, frequency 1 (Hz); F_2, frequency 2 (Hz); F_3, frequency 3 (Hz); F_4, frequency 4 (Hz); D_1, duration 2 (ms); D_3, duration 3 (ms). All frequencies were uniformly lowered by the half-speed recording.

a multivariate analysis of variance, the Hotelling-Lawley trace statistic indicated that some peent calls produced by a single bird were significantly different across display periods ($P<0.001$). A univariate analysis of variance disclosed that only the variables PULSERT and F_1 differed across display periods ($P<0.05$). Coefficients of variation were low (generally less than 5%, for all variables), indicating relative consistency in calls both within and across display periods.

Variation Among Peent Calls from Different Singing Sites

The degree of overlap among calls from different singing sites over the course of the breeding season was evaluated. A data set was selected which included peent calls recorded on sites for which behavioral indicators strongly suggested that the same bird occupied the site during all display periods when recordings were made. The peent calls were recorded during 8, 8, 10, and 11 display periods on four different sites, including the one on which the male was identified by the light-emitting device. Woodcock displaying on these sites consistently peented in the same spot (within approximately 3 m) after each display flight during a given display period. When peenting occurred in a diurnal covert before the arrival of the bird on a given site, the pre-display peenting area was consistently the same. Peent calls recorded during display periods when more than one bird was believed to be on or near the site were excluded from the analysis, and only calls recorded on or after 14 April (except for calls recorded during one 7 April display period) were included, by which date all migration through Pennsylvania had presumably finished (Liscinsky 1972; unpublished personal observa-

Table 1. *Estimation of variance components (expressed as percentages) for peent calls recorded on four sites, with 8 to 11 display periods per site. One bird was assumed to occupy each site.*

Dependent variable	Estimates of variance explained among: Sites	Display periods on a site	Peents within one display period on a site
TD	63.86	19.67	16.47
PULSERT	61.94	28.85	9.21
F_1	30.96	35.90	33.14
F_2	44.50	29.06	26.44
F_3	37.54	29.37	33.09
F_4	19.92	40.75	39.33
D_1	15.20	29.92	54.88
D_2	58.03	21.10	20.87
D_3	0.00	37.28	64.30

tions of decrease in general activity by excess males on sites by mid-April).

A multivariate analysis of variance indicated that significant differences existed among the peent calls from different sites as well as among the peent calls from a single site ($P<0.001$). A univariate analysis of variance disclosed that differences existed among calls recorded during different display periods for all measurements of peent calls recorded on a single site ($P<0.001$), as well as for all measurements except D_3 among the calls from different sites ($P<0.05$). However, the results of the Duncan's multiple range test indicated significant separation of site means for most variables.

The proportion of the total variation attributable to differences among sites was greater than that accounted for by differences among display periods on a single site for five of the nine variables (TD, PULSERT, F_2, F_3 and D_2; Table 1). Discriminant analysis allowed peent calls to be correctly assigned to their respective sites in 82.11% of the 190 cases (Table 2). The percentage of correctly classified peent calls ranged from 68.9 to 100 for the four sites. For 27 of the 36 misclassified peents, the second prediction by discriminant analysis was that of belonging to their actual group. The variables PULSERT and F_1 contributed most strongly to the first function, whereas TD and PULSERT contributed most strongly to the second function. Considerable overlap existed among peent calls from different sites, despite significant separation among centroids for each site (Fig. 2).

Discussion

Identification of Individual Woodcock

Individual identification is critically important in studies of woodcock mating systems and

Table 2. *Classification by discriminant analysis of peent calls[a] recorded on four sites, with 8 to 11 display periods per site. One bird was assumed to occupy each site. Diagonal values represent correct classifications.*

Singing site	No. of calls	No. of calls classified into each site (% in parentheses): Site 3 No.	Site 3 %	Site 4 No.	Site 4 %	Site 5 No.	Site 5 %	Site 16 No.	Site 16 %
3	40	32	(80.0)	7	(17.5)	0	(0.0)	1	(2.5)
4	45	8	(17.8)	31	(68.9)	0	(0.0)	6	(13.3)
5	50	0	(0.0)	0	(0.0)	50	(100.0)	0	(0.0)
16	55	6	(10.9)	5	(9.1)	1	(1.8)	43	(78.2)

[a] Percent of all peent calls correctly classified: 82.11%.

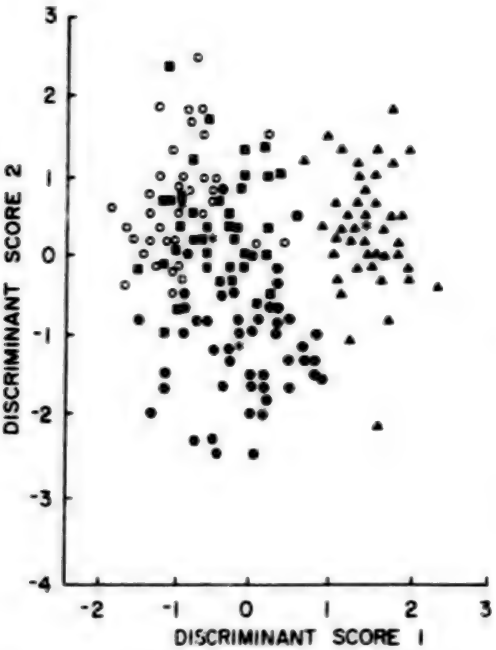

Fig. 2. Graphical representation in standardized discriminant space of peent calls recorded on 4 sites, each represented by a different symbol, with 8 to 11 display periods per site. One bird was assumed to occupy each site. Asterisks represent group centroids.

behavior. Capturing, handling, and marking individuals is time consuming and may affect subsequent survival and behavior. Courting male woodcock usually use the same pre-display peenting area and peenting spot on a site during all display periods at that site. Changes in this behavior signal changes of occupants of particular sites, but these behavioral cues are of no use for later identification of these individuals when they use different sites (Thomas 1975; Bourgeois and Couture 1977).

The present study expanded results from Beightol and Samuel (1973) and Thomas (1975), in which calls of most woodcock were recorded during single display periods. We proceeded from that stage, in which differences among peent calls of given individuals within a single display period were recognized, to a refinement of sonagraphic analysis for possible use in individual identification across display periods or singing sites (or both). We found differences among peent calls recorded from a single site as well as among calls from different sites. However, use of discriminant functions allowed 82.11% (156 of 190) of the peent calls hypothesized to have been produced by four individuals on four particular sites to be correctly classified according to site. These results offer some support to the findings of Beightol and Samuel (1973), Thomas (1975), and Bourgeois and Couture (1977) by confirming that considerable differences exist among the calls of different males.

Previous analyses, and the analysis presented here, indicate that call duration (Beightol and Samuel 1973; Bourgeois and Couture 1977), frequency (Beightol and Samuel 1973; Bourgeois and Couture 1977), and pulse rate are the characteristics most useful in distinguishing among the calls of different individuals. Based on the hypothesis that the overall shape of the call might be an important distinguishing characteristic, additional measurements of frequency and duration, determined by the shape of each particular call, were included in the present analysis. Results indicated that, as a feature peculiar to each individual's call, shape of the call is secondary in importance to pulse rate, initial frequency, and total duration. However, inclusion of these and other measurements (Bourgeois and Couture 1977) in the analysis should considerably increase its accuracy in characterizing the peent calls of individuals.

Exact and highly reliable classification of large numbers of peent calls is far from simple because of variation among the peent calls of a single bird and variations due to both actual differences and bias in the recording due to experimental methods. Experimental procedures that might bias peent-call recordings include variation in the distance between the recorder and the bird and obstacles (such as vegetation) in the sound path between the microphone and the bird (Beightol and Samuel 1973; Thomas 1975). Not only can changes in the position of the woodcock during and between peent calls cause frequency distortion, but also changes in temperature, through effects on tape speed, can cause distortions in recordings of frequency, duration, and pulse rate (Thomas 1975).

Variation among the peent calls of a single bird, coupled with overlap among birds, makes discriminant analysis of peent-call sonagrams an ineffective method for positive identification of individuals and for the monitoring of their movements among sites.

Although Bourgeois and Couture (1977) suggested using sonagraphic analysis of peent calls to monitor the turnover of males on single singing sites, our results suggest that, if used alone, this would be an inexact method for obtaining an accurate count of the number of birds. Sonagraphic analysis used in conjunction with behavioral cues, however, may provide a moderately accurate representation of the degree of male turnover on woodcock singing sites during the breeding season.

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Changes in Habitat Structure on Woodcock Singing Grounds in Central Pennsylvania[1]

by

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Abstract

Fifteen woodcock (*Philohela minor*) singing grounds found in the Bald Eagle Valley in central Pennsylvania and recorded on aerial photographs 20 to 30 years ago were relocated. Fifteen singing grounds now in use were found by walking census routes during 1977. A 0.04-ha plot, centered on the woodcock's primary contact point on the singing ground, was used to delimit a sampling area for describing the habitat on the basis of 40 variables. Mean values for 4 variables were consistent with values for the same variables reported in previous studies. Comparisons of habitat features between new and old singing sites showed that differences in habitat structure resulted from vegetation on old sites being in a later seral stage. Twenty-one variables, showing significant differences between new and old sites, may be useful for determining whether suitable habitat is approaching an unsuitable stage. All 30 sites were correctly classified as either new or old by using a discriminant function consisting of 6 variables: litter cover, density of small woody stems, density of large shrubs, percent bare ground, distance to water, and stand age. The discriminant function may be useful for classifying habitat as suitable or unsuitable. In all, 25 key variables showed potential use for describing suitable habitat, determining if habitat is becoming unsuitable, or classifying habitat as suitable or unsuitable for woodcock singing grounds.

The decline in populations of woodcock (*Philohela minor*) in the Eastern Region since about 1967 (Tautin 1980) may have resulted from habitat loss. To determine if habitat loss is a factor in the decline, we must be able to measure the quantity and quality of habitat available to woodcock.

Identification of woodcock singing habitat requires descriptions of the physical and biological features distinguishing suitable from unsuitable habitat. One approach for recognizing such differences is to compare structural features of singing grounds currently and formerly in use. Such comparisons provide information on the features important in habitat selection by woodcock.

This paper presents information on some of the specific habitat needs of woodcock and reports on differences in habitat structure resulting from plant succession on woodcock singing grounds in central Pennsylvania. The objectives of the study were to: (1) describe some physical and biolog-

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ical features of current woodcock singing grounds in Bald Eagle Valley, Centre County, Pennsylvania; (2) determine if changes in habitat have made singing grounds used in Bald Eagle Valley during 1947 and 1956 unsuitable for woodcock today; and (3) identify variables that may be useful for classifying habitat as suitable or unsuitable.

Bald Eagle Valley

The 1,560-ha study area in Bald Eagle Valley was located along the lower slope of Bald Eagle Mountain and the valley floor south of U.S. Route 220, and extended from the village of Julian to the village of Hannah (Fig. 1). The valley is situated between the foothills of the Allegheny Plateau and the first ridge of the Ridge and Valley Province. The area consists of flat bottomland of alluvial origin with interspersed terraces. Bald Eagle Creek is the primary waterway in the area and parallels U.S. Route 220. Vegetation consists of mixed hardwoods on the upper elevations and scattered hawthorn–crabapple (*Crataegus–Malus*) stands interspersed with hardwoods on the lower slopes. Cultivated areas and dairy farms are situated on the valley floor along both sides of U.S. Route 220. The area was previously described by Yerger (1947), Richter (1948), Miller (1957), Liscinsky (1972), and Kinsley (1981).

Methods

Location of Singing Grounds

Fifteen singing grounds were randomly selected for habitat analysis from a total of 67 active singing grounds found on the study area between 7 March and 12 April 1977. The singing grounds were watched after 15 April to determine the primary contact point on the singing ground where a woodcock landed most often after courtship flights. These 15 singing grounds were termed new singing sites.

Fifteen additional singing grounds were chosen at random from two sets of 65 and 54 singing grounds plotted on aerial photographs during 1947 (Richter 1948) and 1956 (Liscinsky 1972), respectively. Fourteen were selected from 1947 and 1 from 1956. The singing grounds were pinpointed on 1971 aerial photographs (scale 1:12,000) and relocated in the field by triangulation from three permanent objects. The point established by triangulation was considered the primary contact point. These 15 inactive singing grounds were termed old singing sites.

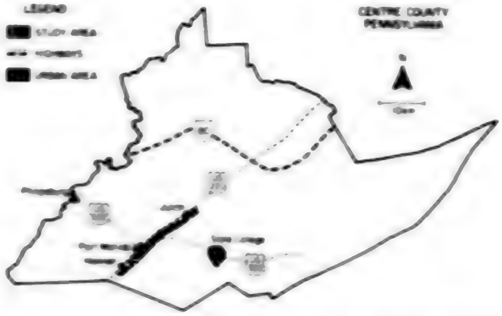

Fig. 1. Location of the study area in Centre County, Pennsylvania.

Habitat Measurements

A square, 0.04-ha plot, with the principal contact point at the center, was established at each singing site to delimit a sampling area for describing habitat. The plot was divided into 100-m^2 quarters which were further subdivided into 25-m^2, 6.25-m^2, and 1.56-m^2 subplots (Fig. 2). Habitat was divided into six strata (Table 1) and sampled by using nested quadrats within a stratified random design as follows. Large-tree, small-tree, and shrub data were collected within the entire plot, two random 25-m^2 subplots in each quarter, and two random 6.25-m^2 subplots in each small-tree subplot, respectively (Fig. 2). Data on ground cover and small woody stems were collected in one randomly selected 1.56-m^2 subplot within each shrub subplot (Fig. 2).

At each singing site, 40 habitat variables were measured (Table 2). Variables were divided into three categories: spatial patterns, vegetative variables, and edge variables. Data were collected between 29 March and 9 December 1978.

Distances and areas were measured with a tape or from aerial photographs. Age and height of overhead cover were based on five dominant stems selected close to the plot center and the center of each quarter. Age was obtained by taking increment cores and counting annual rings or by counting bud-scale scars on small stems. Heights were measured with a tape or

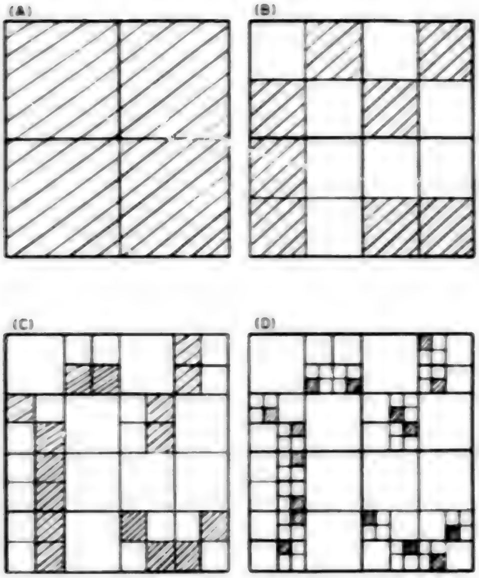

Fig. 2. Stratified random design for sampling large trees (A), small trees (B), large and small shrubs (C), and small woody stems (D) within a 0.04-ha plot.

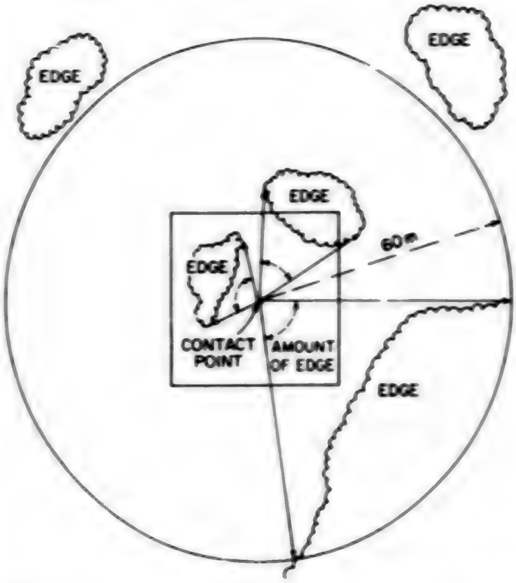

Fig. 3. Example of edge measurements made at woodcock singing sites (Square represents 0.04-ha plot).

altimeter. Percent overhead cover was estimated by taking densiometer readings (Lemmon 1956) at the center of all 25-m² subplots. A 25-intercept point-quadrat frame was used to estimate ground cover (Mueller-Dombois and Ellenberg 1974). Herbaceous height and litter depth were each measured at five randomly selected points within each of the 16 ground-cover subplots. Trees, shrubs, and small woody stems were counted only if rooted within plots. A caliper or diameter tape was used to measure tree diameter.

Table 1. *Definitions of habitat strata.*

Stratum	Definition
Large tree	Woody stem ≥ 2.5 m high and ≥ 7.6 cm DBH
Small tree	Woody stem ≥ 2.5 m high and < 7.6 cm DBH
Large shrub	Woody stem ≥ 1.25 m and < 2.5 m high
Small shrub	Woody stem ≥ 0.3 m and < 1.25 m high
Small woody stem	Woody stem < 0.3 m high
Ground cover	Vegetative or nonvegetative material < 0.3 m high

Distance to edge, edge height, and amount of edge were measured for each quarter and were not limited by the 0.04-ha plot (Fig. 3). Height of edge was the height of the habitat type adjoining the nest or singing site habitat. Edge heights were zero for habitat types containing no vegetation or herbaceous vegetation less than 0.1 m in height. Amount of edge was the amount of edge within 60 m of the principal contact point (Fig. 3). The 60-m limit was based on the approximate radius of the circular area encompassed by a woodcock in courtship flight (Pettingill 1936; Sheldon 1967). Amount of edge was measured by using a range finder and "edge protractor" (Kinsley 1981).

Statistical Analysis

Univariate and multivariate normality were determined from histograms and by plotting normal scores. Non-normal variables were either transformed or excluded from analyses requiring normality. Statistical significance was tested at the 0.10 probability level.

Univariate normal variables were tested for unequal variances and means using variance–ratio and Student's *t* tests, respectively. Non-normal

Table 2. *Definitions of 40 habitat variables measured on new and old woodcock singing sites.*

Variable[a]	Definition
Spatial pattern	
Distance to water	Distance (m) from plot center to nearest water
Distance to diurnal cover	Distance (m) from plot center to nearest known diurnal cover
Distance to nearest singing ground	Distance (m) from plot center to nearest known singing ground
Distance to next nearest opening	Distance (m) from plot center to next nearest opening
Size of opening	Size (m^2) of nearest opening
Size of next nearest opening	Size (m^2) of the next nearest opening
Vegetative variables	
Stand age	Average age of 5 dominant stems
Height of overhead cover	Average height (m) of 5 dominant stems
Percent overhead cover	Average percentage of points with overhead cover from 16 densiometer readings
Small-woody-stem cover	Average percentage of points projecting on small woody stems from 16 point-quadrat readings
Herbaceous cover	Average percentage of points projecting on herbaceous material from 16 point-quadrat readings
Moss and lichen cover	Average percentage of points projecting on moss and lichen from 16 point-quadrat readings
Litter cover	Average percentage of points projecting on litter from 16 point-quadrat readings
Nonvegetative cover	Average percentage of points projecting on nonvegetative material from 16 point-quadrat readings (for this study, it consisted mostly of rock)
Bare ground	Average percentage of points projecting on bare ground and roots from 16 point-quadrat readings
Herbaceous height	Average height (cm) of herbaceous material measured at 16 ground-cover subplots
Litter depth	Average depth (cm) of litter measured at 16 ground-cover subplots
Large-tree density	Total count of large trees per 0.04 ha
Small-tree density	Estimated number of small trees per 0.04 ha from 8 small-tree subplots
Tree density	Estimated number of trees per 0.04 ha (sum of large-tree density and small-tree density)
Basal area	Basal area (cm^2) of large trees per 0.04 ha
Large-shrub density	Estimated number of large shrubs per 0.04 ha from 16 shrub subplots
Small-shrub density	Estimated number of small shrubs per 0.04 ha from 16 shrub subplots
Shrub density	Estimated number of shrubs per 0.04 ha from 16 shrub subplots (sum of large-shrub density and small-shrub density)
Small-woody-stem density	Estimated number of small woody stems per 0.04 ha from 16 ground-cover subplots
Density of large trees < 15.2 cm DBH	Total count of large trees ≥ 7.6 cm DBH and ≤ 15.2 cm DBH per 0.04 ha
Basal area of large trees < 15.2 cm DBH	Basal area (cm^2) of large trees ≥ 7.6 cm DBH and ≤ 15.2 cm DBH per 0.04 ha
Density of large trees > 15.2 cm DBH	Total count of large trees > 15.2 cm DBH per 0.04 ha
Basal area of large trees > 15.2 cm DBH	Basal area (cm^2) of large trees > 15.2 cm DBH per 0.04 ha
Number of tree species	Number of tree species recorded at the 0.04-ha plot
Number of shrub species	Number of shrub species recorded at the 0.04-ha plot
Number of small-woody-stem species	Number of small-woody-stem species recorded at the 0.04-ha plot
Edge variables	
Distance to nearest edge	Distance (m) from plot center to the nearest edge
Height of nearest edge	Height (m) of the nearest edge
Amount of edge	Amount (%) of edge within 60 m of the principal contact point

Table 2. Continued

Variable[a]	Definition
Average distance to edge	Average of the 4 distance-to-nearest-edge measurements (m) taken in each quarter from plot center
Distance to farthest edge	Distance (m) from plot center to the farthest of the 4 edge measurements
Height of farthest edge	Height (m) of the edge farthest from plot center
Distance-to-height ratio for nearest edge	Distance to nearest edge divided by height of nearest edge
Distance-to-height ratio for farthest edge	Distance to farthest edge divided by height of farthest edge

[a]Terms used to name or define variables were defined by Kinsley (1981).

variables were tested for unequal dispersions and medians using Moses Ranklike and Mann–Whitney tests, respectively (Hollander and Wolfe 1973).

Because most multivariate techniques allow only one less variable than sample size, the 40 habitat variables were reduced to 14 by using principle component and partial correlation analyses. Principle component analysis was used to select a reduced number of variables with the potential to differentiate between new and old sites. Variables most highly correlated with the components were selected because they explained most of the information in the components (Amich and Walberg 1975; Morrison 1976; Neff and Marcus 1980). Partial correlation analysis was used to eliminate significantly correlated and conceptually similar variables. If two variables had a partial correlation coefficient >0.75, one was selected as the "better" on the basis of mean difference, equal variance, and normality (Dueser and Shugart 1979; Neff and Marcus 1980).

Discriminant analysis was used to distinguish new and old sites so that their separation on the discriminant axis was a function of their differences in habitat structure. Stepwise discriminant analysis was used to reduce the 14 variables to smaller subsets of variables having a greater discriminatory ability. The discriminant function was validated by applying the jackknife classification procedure.

Data were manipulated and analyzed on an IBM System 370/3033 Processor Complex using the Minitab (Ryan et al. 1976) and SAS (Statistical Analysis System) (Barr et al. 1976) programmed statistical packages. Because no statistical package provided all the necessary information to fully evaluate the discriminant function, we used three statistical packages: BMDP – Biomedical Computer Programs P-series (Dixon and Brown 1977); SPSS – Statistical Package for the Social Sciences (Nie et al. 1975); and SAS.

Characteristics of New Woodcock Singing Sites

Mean values of the 40 habitat variables measured at new singing grounds characterize the physical and biological features of habitat suitable to woodcock. Woodcock accepted a wide range of habitat features at singing sites, as indicated by the large variability in each habitat variable (Table 3).

The values of four variables were found to be consistent with previous studies conducted in other parts of the woodcock's range. The average distance of 92 m from a singing site to diurnal cover was only 4 m greater than that found by Maxfield (1961) and was within the < 183-m distance reported by Sheldon (1967). Mendall and Aldous (1943) found 24 of 29 singing grounds less than 91 m from diurnal cover. Percent overhead cover (14%) was less than the 20 and 60% upper limits used by woodcock in Quebec (Wishart and Bider 1976) and in Minnesota (Marshall 1958), respectively. Stand age (11 years) was less than the 20-year maximum value, and height of overhead cover (3.4 m) was only 0.4 m higher than the upper limit believed tolerated by woodcock in Minnesota (Marshall 1958). The other variables were either inconsistent or were not comparable because of marked differences in definition, technique of measure, or unique application in the present study.

Table 3. *Means and standard deviations of 40 habitat variables measured at 15 new and 15 old woodcock singing sites.*

Variable	New Mean	New Standard deviation	Old Mean	Old Standard deviation
Distance (m) to water	75	41	32	19
Distance (m) to diurnal cover	92	102	120	99
Distance (m) to nearest singing ground	217	129	157	210
Distance (m) to next nearest opening	45	61	20	14
Size (m^2) of opening	9,300	16,095	3,705	10,842
Size (m^2) of next nearest opening	9,986	16,733	6,391	14,542
Stand age (years)	11	8	19	7
Height (m) of overhead cover	3.4	1.8	7.2	2.9
Percent overhead cover	14	19	44	25
Small-woody-stem cover (%)	1	1	1	1
Herbaceous cover (%)	72	21	40	26
Moss and lichen cover (%)	6	6	4	4
Litter cover (%)	17	17	53	26
Nonvegetative cover (%)	1	1	0	0
Bare ground (%)	4	5	2	3
Herbaceous height (cm)	3.2	1.1	2.1	1.2
Litter depth (cm)	1.0	0.9	2.6	1.0
Tree density	54	94	147	130
Large-tree density	3	3	16	12
Basal area (cm^2)	214	217	2,017	1,866
Small-tree density	51	92	131	127
Shrub density	2,823	2,789	3,131	2,481
Large-shrub density	318	344	311	270
Small-shrub density	2,504	2,649	2,819	2,351
Small-woody-stem density	4,186	3,686	5,793	4,407
Density of large trees $<$ 15.2 cm DBH	3	3	14	12
Basal area (cm^2) of large trees $<$ 15.2 cm DBH	200	216	1,198	1,117
Density of large trees $>$ 15.2 cm DBH	0	0	2	2
Basal area (cm^2) of large trees $>$ 15.2 cm DBH	14	55	819	1,006
Number of tree species	4	4	6	3
Number of shrub species	14	7	14	4
Number of small-woody-stem species	13	6	12	4
Distance (m) to nearest edge	5	3	5	5
Height (m) of nearest edge	5.0	3.5	2.6	2.7
Amount (%) of edge	93	14	98	4
Average distance (m) to edge	11	10	12	12
Distance (m) to farthest edge	19	20	24	28
Height (m) of farthest edge	6.2	5.0	3.7	4.0
Distance-to-height ratio for nearest edge	1.4	1.2	0.4	0.7
Distance-to-height ratio for farthest edge	3.9	3.0	3.1	5.0

Differences Between New and Old Singing Habitat

Univariate Analysis

Significantly different mean or median values between new and old sites were found for 21 habitat variables (Table 4). The differences in habitat structure resulted from the vegetation on old sites being in a later seral stage. As at new sites, habitat features at old sites were highly variable (Table 3). Although variable means have shifted along a gradient corresponding to structural changes caused by plant-community development, the variances have not changed.

Table 4. *Significance levels for tests of equal variances, means, medians, or dispersions for 40 habitat variables measured at 15 new and 15 old woodcock singing sites.*

	Significance levels	
Variable	Equal variances or dispersions	Equal means[a] or medians
Distance to water[b,c]	0.1275	0.0010
Distance to diurnal cover[b]	0.7096	0.3054
Distance to nearest singing ground[b,c]	0.0512	0.0912
Distance to next nearest opening[b]	0.0041	0.1365
Size of opening[b]	0.7000	0.1585
Size of next nearest opening[d]	1.0000	0.1776
Stand age[e]	0.8445	0.0112
Height of overhead cover[e]	0.0818	0.0002
Percent overhead cover[b,c]	0.9215	0.0004
Small-woody-stem cover[b]	0.8347	0.7910
Herbaceous cover[c]	0.3844	0.0006
Moss and lichen cover[b]	0.1918	0.3562
Litter cover[b,c]	0.7755	0.0001
Nonvegetative cover[c]	0.0001	0.0674
Bare ground[b]	0.1545	0.4890
Herbaceous height[c]	0.8481	0.0141
Litter depth[c]	0.6122	0.0001
Tree density[b,c]	0.9403	0.0043
Large-tree density[b,c]	0.0417	0.0002
Basal area[c]	0.0031	0.0001
Small-tree density[c,d]	0.4621	0.0043
Shrub density[b]	0.3375	0.5082
Large-shrub density[b]	0.3088	0.7819
Small-shrub density[b]	0.3777	0.4783
Small-woody-stem density[b]	0.9350	0.2515
Density of large trees < 15.2 cm DBH[b,c]	0.0235	0.0016
Basal area of large trees < 15.2 cm DBH[b,c]	0.0129	0.0018
Density of large trees > 15.2 cm DBH[f]	–	–
Basal area of large trees > 15.2 cm DBH[f]	–	–
Number of tree species[b,c]	0.0333	0.0474
Number of shrub species	0.0779	0.8009
Number of small-woody-stem species	0.1112	0.8602
Distance to nearest edge[b]	0.0464	0.4967
Height of nearest edge[c]	0.7000	0.0890
Amount of edge[d]	0.4000	0.0327
Average distance to edge[b]	0.2431	0.9613
Distance to farthest edge[b]	0.2504	0.7146
Height of farthest edge[b,c]	0.2818	0.0490
Distance-to-height ratio for nearest edge[b,c]	0.7937	0.0003
Distance-to-height ratio for farthest edge[b]	0.0623	0.1270

[a] Satterthwaite's approximation was used to compute the degrees of freedom for the *t* test when variances were unequal (Barr et al. 1976; Cochran 1963).

[b] Transformed by $\sqrt{X}$.

[c] New and old sites significantly different ($P < 0.10$).

[d] Variables tested for unequal dispersions and medians using nonparametric Moses ranklike and Mann-Whitney tests, respectively.

[e] Transformed by $3\sqrt{X}$.

[f] No parametric or nonparametric test exists [illegible] he data. Only one new singing site had a tree greater than 15.2 cm DBH; therefore, this variable was [illegible] onstant (0) for new singing sites.

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Variables related to the presence of trees were significantly different at new and old sites (Table 4). Total tree density and basal area were about 3 and 10 times greater on old sites, respectively, with a higher proportion of trees in the 7.6- to 15.2-cm DBH class (Table 3). Large- and small-tree densities were about 5 and 2.5 times greater on old sites, respectively. Old sites also had more species of trees. Vegetation was significantly older, higher, and covered more area on old sites. New sites were characterized by larger amounts of herbaceous cover, whereas old sites had more litter cover.

Differences in amount of edge and edge heights also indicated differences in seral stage. The amount of edge surrounding old singing sites was greater because of the encroachment of vegetation. Edge heights were lower for old sites because about half of the old singing-site contact points were in wooded situations near edges created by openings. Edge height for an opening was zero; thus, a lower mean value resulted for this variable. The mean value for the distance-to-height ratio of nearest edge was significantly lower for old sites because an arbitrary value of zero was assigned when edge height was zero.

Distance to water and distance to the nearest singing ground were significantly less for old sites. The relation between the two variables and seral stage resulted from a combination of land-use history, woodcock behavior, and plant-community development. Examination of aerial photographs revealed that before the 1940's, woodcock habitat was restricted to areas too wet for agriculture. When farming was abandoned, more habitat became available at greater distances from water. Thus, more new sites are farther from water than old sites. As woody vegetation came to dominate old singing grounds, woodcock moved to nearby openings but maintained an association with the old sites. Today, singing males are located close to old sites but maintain wider distances between active sites.

The 21 variables showing significant differences between new and old sites may prove useful for determining when suitable habitat is becoming unsuitable. Old sites were unused during the present study, and many sites were clearly unusable because of large amounts of vegetative cover. Although these variables indicate differences between suitable and unsuitable habitat, they cannot be used to classify habitat because no one variable can completely describe differences between new and old sites. Discriminant function analysis was used to classify habitats on the basis of a combination of discriminating variables.

Reduction of Variables

Eleven principal components accounted for 90.2% of the total variance in habitat measurements. Correlations of variables with the components were ordered from highest to lowest (regardless of sign), breaks were found, and variables with larger coefficients were selected for further analysis. Seventeen of the 40 habitat variables were selected for partial correlation analysis.

Three correlation coefficients >0.75 were found: average distance to edge was correlated with distance to farthest edge; herbaceous cover was correlated with litter cover; and small-woody-stem cover was correlated with small-woody-stem density. Distance to farthest edge, litter cover, and small-woody-stem density were selected as the "better" variables. Fourteen variables remained for discriminant analysis.

Discriminant Function Analysis

The stepwise discriminant analysis resulted in a significant discrimination ($P<0.0001$) between new and old singing sites based on six habitat variables. The null hypothesis of equal covariance matrices could not be rejected ($P=0.98$).

The contribution of each habitat variable to the discriminant function was determined from the standardized discriminant function coefficients (Table 5). Litter cover was the most important variable differentiating new and old sites. Small-woody-stem density, large-shrub density, bare ground, distance to water, and stand age were the next five important variables, respectively.

The weighting of each discriminatory variable toward new or old sites was determined from the signs of the standardized discriminant coefficients and the values of the classification functions coefficients (Table 5). Small-woody-stem density, large-shrub density, bare ground, and distance to water were weighted toward new sites. All other things being equal, large values for these four variables increased the likelihood of a site being classified as a new singing site.

Table 5. *Standardized discriminant function and classification-function coefficients for discriminating between new and old woodcock singing sites.*

Importance rank	Variable	Standardized coefficient	Classification coefficient	
			New	Old
1	Litter cover	-1.53804	-1.65361	1.22015
2	Small-woody-stem density	0.86115	2.52412	0.64895
3	Large-shrub density	0.73205	2.06068	-0.46927
4	Bare ground	0.69964	3.23513	0.78059
5	Distance to water	0.67721	2.44180	1.22223
6	Stand age	-0.58978	-0.05171	0.24600
	Constant		-16.52339	-12.00759

Litter cover and stand age were weighted toward old sites. All other things being equal, large values for these two variables increased the likelihood of a site being classified as an old singing site. The nature of the variables comprising the discriminant function indicated that new singing sites were located in an earlier seral stage characterized by less litter cover, more small woody stems and large shrubs, more bare ground, greater distance to water, and younger stands.

The decrease in distance to water from new to old sites has already been discussed. A similar decline in amount of bare ground was related to the land-use history of the study area. Overgrazing in the past left many barren areas on the abandoned fields. During the present study, woodcock often selected these spots for their singing grounds. Old sites had less bare ground because of colonization by herbaceous and woody vegetation.

All sites were correctly classified by the discriminant function indicating complete separation between groups (Table 6). The rapid development of woody cover in early seral stages was probably the most important factor contributing to the complete separation of groups. Open habitats such as singing grounds could become forested in 30 years, especially if invaded by fast-growing species such as aspen (*Populus* spp.). Twenty-nine sites (96.7%) were correctly classified by the jackknife procedure (Table 6). Because the classification of the jackknife did not differ greatly from the classification of the regular function, the discriminant function was considered an accurate measure of differences between new and old sites.

Assuming that old sites were unsuitable for singing males, we can estimate the rate of suitable habitat loss. The complete separation between groups indicated that after 30 years, plant-community development will have progressed sufficiently to make currently active sites unsuitable for woodcock. The loss of all current singing sites over 30 years would represent a loss of 3.3% per year. The 3.3% annual loss is a conservative estimate because it is unknown when old sites became unsuitable. The wide separation between groups indicated that old sites were probably unusable several years before the present study was conducted. Sheldon (1967) reported the annual singing-ground loss through plant-community development to be 8.5% for 67 singing grounds in Massachusetts.

Use of the Discriminant Function

The singing-site discriminant function could prove useful for habitat classification and management. It should be possible to sample areas similar to those examined in this study and to classify habitat as suitable or unsuitable. Var-

Table 6. *Classification of the 30 woodcock singing sites into new and old singing habitat, using 6 habitat variables.*

Analytical method, type and no. of sites	Site classification			
	New		Old	
	No.	%	No.	%
Classification procedure				
New, 15	15	100	0	0
Old, 15	0	0	15	100
Jackknife procedure				
New, 15	14	93.3	1	6.7
Old, 15	0	0	15	100

Table 7. *Variables showing potential use for identifying habitat needs of woodcock.*

	Use		
Variable	Describing habitat	Determining unsuitability	Classifying habitat
Spatial pattern			
Distance to water		X	X
Distance to diurnal cover	X		
Distance to nearest singing ground		X	
Vegetative variables			
Stand age	X	X	X
Height of overhead cover	X	X	
Percent overhead cover	X	X	
Herbaceous cover		X	
Litter cover		X	X
Nonvegetative cover		X	
Bare ground			X
Herbaceous height		X	
Litter depth		X	
Tree density		X	
Large-tree density		X	
Basal area		X	
Small-tree density		X	
Large-shrub density			X
Small-woody-stem density			X
Density of large trees < 15.2 cm DBH		X	
Basal area of large trees < 15.2 cm		X	
Number of tree species		X	
Edge variables			
Height of nearest edge		X	
Amount of edge		X	
Height of farthest edge		X	
Distance-to-height ratio for nearest edge		X	

iables comprising the function could be useful indicators for determining when singing grounds approach the unsuitable stage. Subsequently, habitat could be manipulated to create favorable conditions for woodcock.

In summary, 25 variables have shown potential use for either describing suitable habitat, determining if habitat is becoming unsuitable, or classifying suitable and unsuitable habitat (Table 7). These variables should be considered for inclusion in future studies of woodcock singing habitat because they show potential for identifying the habitat needs of the species.

Conclusions

1. Although all variables described suitable singing habitat in Bald Eagle Valley, four variables (distance to diurnal cover, percent overhead cover, stand age, and height of overhead cover) showed potential for describing habitat on a regional scale; mean values for these variables were in accord with results of other studies conducted in other parts of the woodcock's range.

2. Plant-community development during a 30-year period was sufficient to convert suitable habitat into an unsuitable stage; 21 variables that showed significantly different mean or median values between new and old sites may be used to determine when suitable habitat is becoming unsuitable.

3. A discriminant function consisting of six variables (litter cover, small-woody-stem density, large-shrub density, bare ground, distance to water, and stand age) may be useful to classify woodcock singing habitat as suitable or unsuitable.

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Differential Use of Woodcock Singing Grounds in Relation to Habitat Characteristics[1]

by

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Abstract

During spring and summer 1979, woodcock (*Philohela minor*) singing grounds were studied to determine whether there was a relation between habitat features and the frequency with which sites were used by displaying males. Twenty singing grounds in central Pennsylvania were visited 16 times by investigators during the dusk performance from mid-March to late April. For each singing ground, a use index was calculated as the fraction of visits during which a displaying woodcock was present. Habitat analyses conducted from late May to early August consisted of vegetative, spatial, physiographic, and edge measurements made within and around a 0.04-ha plot centered on the male's principal landing spot. Stepwise linear regression was used to relate the use index to these habitat characteristics. A multiple correlation coefficient of 0.88 was found between the use index and edge height, shrub density, and opening size. Because they are related to frequency of use, these habitat variables may determine the quality of active woodcock singing sites.

Earlier investigations (Mendall and Aldous 1943; Sheldon 1967; Lambert and Barclay 1975; Wishart and Bider 1976; Kinsley et al., this volume) have provided quantitative descriptions of singing-ground habitat and have helped to determine the range of habitat features that is acceptable to displaying male woodcock (*Philohela minor*). However, little is known of the factors that determine the quality of otherwise usable habitat. Presumably, site quality should be reflected in the breeding success of the displaying male. Thus, one might expect that better-quality sites would be frequented by older, more dominant birds, occupied more consistently from one year to the next, and used more frequently in a single singing season.

We measured the frequency of use of woodcock singing sites during one season as an index to site quality. Although physical and biological factors other than site characteristics may affect the frequency of site use, only the relation between the use index and habitat features was examined in this study. The composition of plant communities on singing grounds varies throughout the breeding range, suggesting that no particular species are important in determining site occupancy by displaying males (Wishart and Bider 1976). Consequently, vegetative structure and spatial and physiographic features were the focal points of this analysis. Our objective was to identify variables that might be used to assess the quality of usable singing-ground habitat.

Methods

Site-Use Index

From 18 March to 26 April 1979, we made 16 visits to each of 20 woodcock singing grounds on State Game Lands 176 in Centre County, Pennsylvania. The use of each singing ground by displaying woodcock was recorded on two randomly selected evenings during each of eight consecutive five-day periods. Each observer visited two or three sites each evening within a 30-min period. The sampling period began either when the first peent was heard or 15 min after sunset,

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whichever was earlier. For each singing ground, a use index was calculated as the decimal fraction of the 16 visits during which a displaying woodcock was present. Several sites that were not used in 1979 were assigned a use index of zero; however, for the purposes of this study, these sites were considered active singing grounds because they had been used in 1978 and in previous years.

Habitat Analyses

From 28 May to 3 August 1979, singing-ground habitats were analyzed by methods described by Kinsley et al. (this volume). Measurements were obtained within and around a square 0.04-ha plot centered on the male's principal landing spot. Briefly, the method involved the measurement of 26 vegetative variables (including ground cover and overhead cover, basal areas, and stem densities), 6 spatial variables (including distances to water and the nearest used singing ground, and opening sizes), and 8 edge variables (including edge heights and distances to edge). The habitat analyses also included measurements of two physiographic variables (slope and elevation). Slope was defined as the maximum percent ratio of vertical to horizontal distance across the 0.04-ha plot along a line perpendicular to one of its sides. An Abney level was used to measure slope to the nearest percent. Elevation was defined as the height of the principal landing spot above sea level. Aerial photographs and a topographic map were used to determine elevation to the nearest meter. Distance to diurnal cover was not measured.

Statistical Analyses

Stepwise linear regression (Neter and Wasserman 1974) was used to examine the relationship between the use index and habitat characteristics. The STEPWISE procedure of the Statistical Analysis System (SAS) (Barr et al. 1979) was used, and the significance levels for adding and removing variables were set at 0.50 and 0.10, respectively. To avoid prediction bias and to eliminate variables that did not contribute greatly to the descriptive power of the model, only those variables that accounted for a substantial increase in R^2 were retained. The identification of these variables was facilitated by plotting R^2 versus the number of variables in the model (Neter and Wasserman 1974). Spearman rank-order correlations among the independent variables in the final model were obtained by using the SAS CORR procedure (Barr et al. 1979). These correlations were calculated to determine whether multicolinearity (Neter and Wasserman 1974) existed. Nonparametric correlation coefficients were necessary for this step because two of the variables were not considered to be from normal distributions (Nie et al. 1975). The aptness of the final model was studied by examining the residuals (Neter and Wasserman 1974).

Results

Three habitat variables accounted for most of the variation in the use index. A significant ($F = 22.4$, $P = 0.0001$) relation was found between the use index and height of farthest edge, shrub density, and opening size. The range, mean, and standard deviation for each of these variables are presented (Table 1) to describe the data from which this relation was derived. The multiple correlation coefficient was 0.88. The t-ratios (Neter and Wasserman 1974) indicated that the use of singing sites was correlated negatively with opening size ($t = -3.35$, $P = 0.004$) and height of farthest edge ($t = -5.70$, $P = 0.0001$) and that it was correlated positively with shrub density ($t = 4.45$, $P = 0.0004$). A Spearman rank-order correlation matrix revealed no significant correlations ($P > 0.12$) among these three habitat variables, indicating the absence of multicolinearity effects. From residual analyses, there was no evidence that the assumptions of the model were violated.

The chances of obtaining meaningless correlations increase as the number of variables con-

Table 1. *Summary statistics for the use index and the first three singing-ground-habitat variables found to be significant using stepwise regression.*

Variable	Range	Mean	Standard deviation
Use index	0.00–0.94	0.31	0.34
Height of farthest edge (m)	1.4–16.2	5.7	4.3
Shrub density (stems/0.04 ha)	2,112–18,880	8,634	4,569
Opening size (m^2)	43–56,195	6,404	13,414

sidered gets larger. Thus, entering the 42 habitat variables into the STEPWISE program increased the chance of obtaining spurious correlations between the use index and habitat characteristics. However, as the following section indicates, the relations described above are consistent with the literature, suggesting that they are not spurious.

Discussion

Singing-Ground Use in Relation to Habitat Characteristics

Height of Farthest Edge

The inverse relation between height of farthest edge and singing-ground use suggests that tall vegetation near singing grounds reduces site quality. A high edge bordering a singing ground presents a barrier to the low-trajectory ascent of the woodcock's display flight, whereas a lower edge would allow for exit routes that are more conducive to the bird's low initial flight. Lambert and Barclay (1975) found that sites encircled by high, dense vegetation did not get extensive use, and they suggested that this was due to the lack of suitable flight paths. Sheldon (1967:63) emphasized the woodcock's need for such exit routes, and he noted that tall surrounding edges "may limit the usefulness of an otherwise good singing site." Thus, edge height in the direction of potential flight paths may determine the quality of a singing ground by influencing the number of suitable exit paths from that site.

Shrub Density

The frequent use of shrubby sites suggests that higher shrub densities improve singing-ground quality. Higher stem densities may improve site quality by providing increased protection from avian predators. Sheldon (1967) and Godfrey (1974) discussed observations and circumstantial evidence that implicate owls as predators of male woodcock on singing grounds. Avian predation could have led to a preference for sites with higher shrub densities. Information from previous studies also suggests that this preference exists. Mendall and Aldous (1943), Sheldon (1967), and Weeks (1969) found that many singing grounds had at least a scattering of shrubs on them. Wishart and Bider (1976:528) reported that "the structure of persistent cover in fields determined their use by woodcock, and pastures without woody vegetation were not frequented." They concluded that woodcock apparently "use clearings without shrubs only when suitable fields are limited in number." Thus, shrubbier sites may be of higher quality because the higher stem densities would tend to foil aerial attacks. Exceedingly dense vegetation, however, may reduce the quality of a site by hampering the bird's ability to make its courtship flight (Wishart and Bider 1976).

Opening Size

The frequent use of smaller openings indicates that opening size may affect site quality. However, the relation between opening size and shrub density ($r = -0.35$, $P = 0.13$) and the frequent use of shrubby sites suggest that smaller openings were used more consistently because of their favored vegetative structure, rather than their size. Mendall and Aldous (1943) noted that the size of singing grounds varied widely and that no preference for any particular opening size was evident. Subsequent reports (Sheldon 1967; Wishart and Bider 1976) agreed with these observations. Thus, although there may be a minimal opening size that is acceptable (Mendall and Aldous 1943), opening size per se does not appear to be important in determining the quality of singing sites.

Conclusion

Before habitat-manipulation plans based on these apparent relations can be implemented, their validity must be confirmed. By proposing relations that can and should be tested, this study serves as a starting point in a variable-identification process, which may ultimately provide a means of assessing the quality of singing-ground habitat. Once managers know which characteristics determine the quality of woodcock singing grounds, the effectiveness of habitat-manipulation practices can be improved.

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Examination of Woodcock Nest Sites in Central Pennsylvania

by

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Abstract

Evidence is given to support low selectivity in choice of nest sites by woodcock (*Philohela minor*). Habitat characteristics measured at 30 woodcock nest sites were compared with non-nest control sites in Huntingdon County, central Pennsylvania. Mean nest density per year was 1/4.8 ha within the 54-ha study area. Of 14 characteristics measured, higher shrub-stem density at nests was the only variable significantly different ($P < 0.05$) from controls by univariate *t*-test. A multivariate *t*-test showed no significant difference ($P > 0.05$) between habitat characteristics at nests and controls. A computed discriminant function also indicated little distinction between nests and controls. Spatial distribution of nests for each of the three years did not depart significantly ($P > 0.05$) from a random distribution. Although evidence is given for little overall selectivity, greater shrub-stem density at nests and associations related in part to "edge" habitat may be important in the location of substantial numbers of woodcock nests. The mean distance from nest site to nearest tree (1.0 ± 1.1 m) and to nearest shrub (22.8 ± 17.8 cm) was significantly less ($P < 0.01$) than for control areas. Additional research on woodcock nest-site selection may lead to enhanced woodcock production in a variety of habitats.

Habitat research on the breeding grounds was an important priority when the first national management plan for American woodcock was prepared (Liscinsky 1966), and it remains one of the important priorities in the recently proposed 10-year management plan (Owen 1974, 1977). Nesting habitat has been described for various parts of the woodcock breeding range: in New York (Pettingill 1936), Maine (Mendall and Aldous 1943), Massachusetts (Sheldon 1967), Pennsylvania (Liscinsky 1972), and West Vir-

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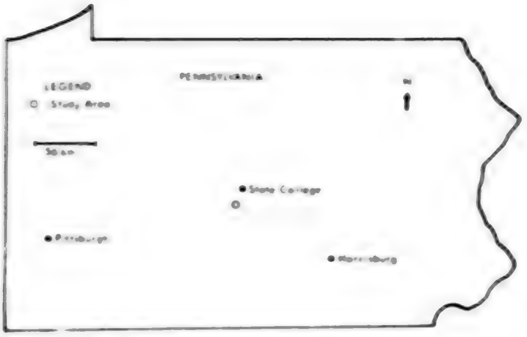

Fig. 1. Location of study area in central Pennsylvania.

ginia (Kletzly 1976). Recent work has described woodcock habitat in terms of vegetative structure, with emphasis on quantitative comparisons (Wenstrom 1974; Wishart and Bider 1976; Kroll and Whiting 1977; Morgenweck 1977), including nesting habitat (Causey et al. 1974; Clauson 1974; Chambers 1976; Bourgeois 1977; Gregg and Hale 1977; Rabe 1977).

The objectives of the present study were: (1) to test the null hypothesis of no difference in habitat characteristics between woodcock nest sites and randomly chosen control sites, (2) to identify and describe physical and vegetational characteristics important for nest site selection by woodcock, and (3) to examine the spatial relations among woodcock nests.

Location

Nest searches were conducted on a 54-ha area (Charter Oak) in The Pennsylvania State University Experimental Forest about 16 km south of State College in Huntingdon County (Fig. 1). A description of the area was provided by Henry (1969). Charter Oak has been an important area for woodcock, providing a good mixture of singing, nesting, feeding, and diurnal habitat. Experimental plantings, cuttings, and other treatments have been carried out for woodcock management purposes (Liscinsky 1955, 1972). The area has both well drained and poorly drained sites, and harbors pure and mixed stands of pine and hardwoods (Fig. 2).

Nest Searches

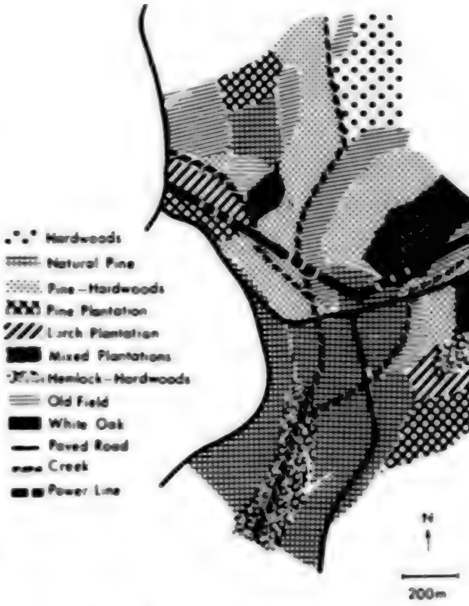

Fig. 2. Map of the Charter Oak study area showing types of cover in The Pennsylvania State University Experimental Forest.

The area was searched systematically by two to four men with three to four trained pointing dogs; the only areas avoided were the interior portions of a stand of nearly pure white oak (*Quercus alba*), two pine (*Pinus resinosa*) plantations, and two larch (*Larix decidua*) plantations, a total of 14 ha. Although these areas were not searched because of lack of suitable ground cover and lack of previous nest records, occasional trips were made through them. All nest searches took place in the morning during April and May at intervals of 4 to 7 days: 9 searches were made in 1972, 12 in 1973, and 14 in 1974.

Vegetation Analysis and Nest Placement

Our method of vegetation analysis was patterned after that of James and Shugart (1970); it was used by James (1971), Whitmore (1975), and others to analyze habitat differences for bird species. Sample plots were 0.04-ha (0.1 A) circles (radius, 11.3 m) with the nest at the center. At each plot the following measurements were made: (1) percentage of available light, (2) soil moisture, (3) distance to nearest edge, (4) amount of edge in plot, (5) distance to nearest man-made edge, (6) maximum canopy height, (7) canopy cover, (8) number of shrubs, (9) number of tree species, (10) total number of trees present, (11) basal area of trees (trees < 2.5 cm DBH were considered to be 2.5 cm DBH for basal area measurements), (12) number of trees < 2.5 cm DBH, (13) number of trees 2.5 to 15.2 cm DBH, and (14) number of trees > 15.2 cm DBH.

Spatial relations that were measured were distances between (1) nest sites active the same year, (2) nest sites and the nearest shrub, and (3) nest sites and the nearest tree.

Trees were considered to be any woody stem taller than 1.8 m, regardless of diameter. Shrubs were woody stems 1.8 m or less. Light measurements were taken with a Gossen Lunasix light meter (King Photo Corp., Woodside, New York). The reading obtained at the nest site (plot center) was divided by the reading taken in the open with no canopy to give the percentage of light falling on the plot compared to the total amount available. Soil moisture was measured with a model 2900 Soil Moisture Probe (Soilmoisture Equipment Company, Santa Barbara, California); this device enabled direct comparison of moisture in various types of soil.

An edge was considered to be a distinct break in forest, shrub, or open-field vegetation. Edges on the study area were roads, trails, powerline rights-of-way, stream banks, field edges, and natural breaks in the canopy between forest stands and forest openings.

Control plots were located by placing a grid containing 214 squares (0.25 ha each) over a map of the study area and selecting 15 plots from a table of random numbers.

Measurements were made during the summer months after the nesting season. Although the time delay between nest selection and use, and subsequent analysis, may have resulted in a bias in the actual value for some parameters (e.g., light intensity, soil moisture, and canopy cover), the comparison of treatment and control considered the relative difference in values.

We employed the method of Clark and Evans (1954) to examine the dispersion of woodcock nests present each year. An R value was computed that used the distance between nearest neighbors (Clark and Evans 1954:447). The R value is a measure of the degree to which the observed distribution departs from random. If nests are randomly distributed, R equals 1. If nests are clumped or aggregated, R approaches 0. If there is uniform spacing between nests, R is greater than 1. The statistical significance of departures from R = 1 was tested by using the normal curve, following the Clark-Evans model. The standard variate of the normal curve was used in determining the probability.

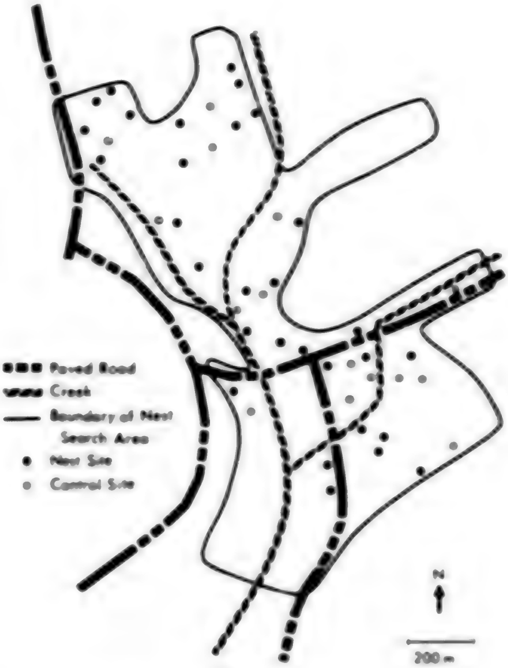

Fig. 3. Location of 30 woodcock nest sites and 15 control sites on the Charter Oak study area.

Nests

During 1972-74, 34 woodcock nests were located; of these, 30 nest sites were later relocated and plotted for statistical comparison with the 15 control sites (Fig. 3). Nests were located at the rate of one per 9.2 dog-hours, or one every 2.5 h in the field (Table 1). Each search period also lasted nearly 2.5 h, so a mean of one nest was located per search day. The mean number of nests located each year was 11.3, and the mean density of nests per year was 1/4.8 ha. The high density of nests on the Charter Oak area is in contrast to the extremely low nest density on nearby State Game Lands 176. From one to five search areas, varying in size from 3 ha to about 60 ha, were searched with pointing dogs during eight trips totaling 21 h, from 1972–74. No nests were found there, even though the mean number of

Table 1. *Results of woodcock nest searches on Charter Oak study area of The Pennsylvania State University Experimental Forest.*

Variable	1972	1973	1974	Mean
No. of trips	9	12	14	11.7
No. of hours	25	26	33	28.0
Dog-hours[a]	122	91	99	104.0
No. of nests	11	11	12	11.3
Dog-hours/nest	11.0	8.3	8.2	9.2

[a] One hour of work by one dog is 1 dog-hour.

singing males present along the 13-km access road each year was 15. From 7 to 9 singing males were present each year at Charter Oak.

Comparison of Nest and Control Sites

Nest and control plots fell with similar frequency in three broad cover types (Table 2). The means for only 1 of the 14 variables differed statistically by univariate *t*-test. Shrub–stem density was significantly ($P<0.05$) greater at nests than in control areas. We then applied the Hotelling T^2 statistic, the multivariate form of the Student's *t*-test (Morrison 1967). We compared the two sets of habitat measurements (Table 3) and tested the null hypothesis of no difference between nest sites and control sites. The hypothesis was not rejected at the 0.05 level ($0.05<P<0.10$).

Table 2. *Relations of nest sites and control sites to cover type and canopy cover.*

Type of site and number	Site characteristics					
	Forested; nearly closed canopy		Brushy edges; medium canopy		Openings; nearly open canopy	
	No.	%	No.	%	No.	%
Nest (30)	10	33	9	30	11	37
Control (15)	5	44	4	27	6	40

Table 3. *Means and standard deviations of habitat variables measured in 0.04-ha plots at 30 woodcock nest sites and 15 control sites.*

Variable	Nest		Control	
	Mean	S.D.	Mean	S.D.
1. Percentage of available light	93.8	4.5	95.0	6.0
2. Soil moisture (mb)	7.6	7.1	7.6	4.5
3. Distance (m) to nearest edge	9.4	10.4	13.7	12.5
4. Amount of edge in plot (m)	15.2	17.4	8.5	9.8
5. Distance (m) to nearest man-made edge	72.8	66.8	87.1	79.8
6. Maximum canopy height (m)	11.0	4.3	11.6	9.1
7. Canopy cover (%)	19.2	9.1	22.9	9.8
8. No. of shrub stems in 0.008 ha subplot	394	226	230[a]	129
9. No. of tree species in plot	6	3	7	3
10. No. of trees in plot	49	41	74	58
11. Basal area (m^2)	0.24	0.22	0.20	0.18
12. No. of trees < 2.5 cm DBH	23	29	42	53
13. No. of trees 2.5 to 15.2 cm DBH	22	19	29	21
14. No. of trees > 15.2 cm DBH	4	5	3	3

[a] $P < 0.05$.

These test results indicated that nest plots were not obviously and sharply distinguishable from randomly chosen control plots, and that woodcock do not appear to be restrictive in their requirements for nest site location, considering the site as the entire 0.04-ha circle (the positioning of the nest within the plot is discussed later). Indeed, some control plots may have contained nests in the past and could do so in the future.

Since the differences between nest and control plots approached significance, we felt that further comparisons would be useful. It seemed probable that woodcock did not nest at random on the study area because of their apparent association with higher stem density of shrubs, lower tree density, and proximity to an edge: 95% of the nests were within 20 m of an edge. In New York, Chambers (1976) and Clauson (1974) reported that 7 nests were 17 ± 14 m from the nearest herbaceous opening. In Michigan, Bourgeois (1977) recorded a mean distance of 7 ± 4 m to the nearest edge for 16 nests.

Multivariate Discriminant Analysis

Since the multivariate analysis showed no significant differences between groups, whereas the univariate analyses indicated significance for at least one variable, we investigated group differences for subsets of variables. The two-group stepwise discriminant function (Jennrich 1977) was used to: (1) discover those combinations of habitat features which best highlight group differences, (2) develop a classification function for use in identifying the nesting potential of new sites, and (3) assess the classification accuracy of this function. The rate of correct classification depends on the similarity of habitat features among groups; for quite distinct groups the rate may be expected to be high.

Shrub–stem density was selected first by the stepwise procedure, on the basis of univariate group differences. It was followed in order by percentage of light, amount of edge, canopy cover, and number of trees in the largest size category. The importance of these variables was determined by a comparison of the full discrimination function with one from which individual variables were deleted. The order of importance was, in fact, identical to the order of entry, except that percentage of light was least important. This finding stems from the high correlation of light with the remaining habitat features, so the deletion does not result in a substantial decrease in discriminatory power.

The discriminant function was also evaluated by its accuracy for classifying sites into groups. A jackknife classification procedure (Lachenbruch 1967) was used to assess the rate of correct classification, based on 30 nest plots and 15 control plots. Of the 30 nest plots, 21 (70%) were correctly classified, as were 11 (73%) of the 15 control plots. The overall rate was 71%, indicating that this discriminant function could correctly classify random plots of woodcock habitat with 71% accuracy. By chance alone, however, we would have expected 55% accuracy in classification ability based on the sample sizes we used (Cohen 1960, 1968).

To eliminate the bias inherent in stepwise procedures (Hocking 1976), and to provide additional information with which to select the important variables, we used a second approach which considers discriminant functions for all possible combinations of variables (McCabe 1975; McCabe and Pohl 1973). In this method we ask a series of questions, "Given only one variable, which one is best able to discriminate between the groups?" We ask this again for two variables, for three, for four, and so on. The most important single variable was shrub–stem density (No. 8, Table 3); the best two variables were light and shrub stems; the best three were shrub–stem density, the amount of edge, and the number of trees > 15.2 cm DBH. The best four were amount of edge, canopy cover, number of trees, and basal area of trees.

The collection of features given by stepwise discriminant analysis closely matched those produced by the all-discriminations procedure and had approximately the same discriminatory power. The all-discriminations procedure necessarily outperformed the stepwise procedure when evaluated by the significance of group differences, though error rates in stepwise discriminant analysis were occasionally lower. Overall, the two procedures produced comparable results, both in the selection of variates and in their assessment.

Nest Placement in Plot

Two additional variables were measured to describe nest placement within the plots more closely. Before taking measurements, we observed that nests were typically located within 1 or 2 m of the base of a tree or shrub. Such nest placement has been cited previously (Sheldon 1967; Clauson 1974), but no quantitative data are available. We measured the distance from each nest and control site to the nearest tree and nearest shrub. The mean distance from nest site to tree (1.0 ± 1.1 m) and from nest to shrub (22.8 ± 17.8 cm) was significantly less ($P < 0.01$) than for controls. Controls were 3.2 ± 4.9 m from the nearest tree and 81 ± 112 cm from the nearest shrub – a substantial difference. This departure suggests that, within suitable nesting habitat, woodcock are selective as to actual placement of the nest in relation to surrounding trees and shrubs.

Dyer and Hamilton (1977) indicated that woodcock prefer a narrow range of light intensity for diurnal cover. This phenomenon was evident for nests, particularly near or within openings where nest placement 1 m or more away from the nearest tree (shrub) would expose the nest to a sharp change in canopy cover and, therefore, in light intensity. Nests located on forested edges, where there was rather continuous canopy cover, were farther from the nearest tree or shrub than nests in openings.

Spatial Distribution of Nests

Three patterns can generally be recognized for describing spatial relations of populations, in this instance woodcock nests: (1) random, (2) uniform spacing (maximum distance between nests), and (3) clumped or aggregated (Odum 1959).

The dispersion of nests did not vary significantly ($P > 0.05$) from random for any of the three years (Table 4). There was no consistent tendency toward either a uniform or clumped distribution.

Discussion and Conclusions

Previous research in Pennsylvania, as well as in other states, found low selectivity for woodcock nest location. Liscinsky (1972) indicated that woodcock use a wide variety of cover types in Pennsylvania and that nest site requirements are few. Mendall and Aldous (1943:89) stated that in Maine, "The cover that immediately surrounds the nests is so varied in both type and extent as to discourage correlations." Sheldon (1967) reported that in Massachusetts, woodcock nests were found in abandoned fields, conifer plantations, brushy areas, mixed forests of all ages, and blueberry fields. Chambers (1976) found 17 nests in eight types of cover in New York.

Table 4 [illegible]ial relation among woodcock nests over [illegible]-ha area on *The Pennsylvania State University Experimental Forest, Huntingdon County, Pennsylvania.*

	Year		
Statistic[a]	1972	1973	1974
N	11	11	12
r_A	340	410	300
r_E	365	365	348
R	0.93	1.12	0.86
c	0.44	0.78	0.86
Probability[b] of a significant departure from random	0.66	0.43	0.39

[a]From Clark and Evans (1954).
[b]$P > 0.05$.

Our data provide additional evidence to support low preference for nest-site selection in woodcock. Nests were neither clumped nor evenly spaced, and their distribution did not depart significantly ($P > 0.05$) from random placement. We suspect the size and positioning of suitable cover types afforded abundant nest-site locations throughout the 54-ha area. The area contained a mixture of singing, nesting, and brood-rearing habitat as well as summer field-roosting habitat that holds woodcock from April to November.

The most important habitat variable that distinguished nest from non-nest areas was shrub-stem density. Significantly ($P < 0.05$) higher stem density at nests may be related to the proximity of nests to "edges" where conditions for increased shrub density are usually more favorable. Nests were located only a short distance from natural and man-made edges (9.4 ± 10.4 m), and the mixture of habitat types on the study area provided an abundance of edge cover. In Wisconsin, 20 of 32 nests were within 10 m of an edge (Gregg 1974), and in Massachusetts, 30 nests were within 46 m of an edge (Sheldon 1967).

We conclude that woodcock do not appear to be sharply selective in choice of nesting cover. However, proximity to an edge, reduced light intensity, distance from the base of a nearby tree or shrub, and especially greater shrub–stem density in the nest area appear to be important factors in the selection of nest sites by woodcock.

These findings confirm the need for continued study of woodcock nest-site selection. Of particular importance is the need for research on the size and positioning of habitat types as they relate to woodcock use. It appears that a mixture of cover types in relatively small blocks of suitable habitat can provide important nesting cover, and that such areas should be maintained to provide for optimum woodcock production.

Acknowledgments

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Woodcock Brood Ecology in Maine

by

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Abstract

Captures of 102 American woodcock (*Philohela minor*) broods, including 338 chicks, from 1977 to 1980 provided data on age-related production by breeding females and on growth and survival of chicks. Although broods of second-year females are smaller and hatch at slightly later dates and the growth of the chicks is slower than that of broods of after-second-year hens, we could detect no difference in survival of the chicks. Yearly variation in the sex ratio of fledged young was probably the result of selection for or against larger female chicks during different environmental conditions. Broodmates associate with each other throughout the summer, and there are differences in habitat preferences between young (1-5 days old) and older (> 5 days old) broods. Older broods prefer more open, mature forest stands with fewer trees per hectare.

Studies of habitat selection by American woodcock (*Philohela minor*) broods have been reported by Wenstrom (1973), Bourgeois [illegible] and Rabe (1977). Information on age-related production by breeding females and on growth and survival of woodcock chicks is more difficult to obtain, however, and requires long-term projects on specific study areas, with large numbers of broods and hens captured annually. A large-scale spring and summer woodcock capture program in operation since 1977 on the Moosehorn National Wildlife Refuge in Maine has yielded new information on these topics. We present observations from that program on age-related aspects of production in adult female woodcock, growth of woodcock chicks, survival of chicks to the post-fledging period, sex ratio of fledged chicks, and age-specific habitat selection by woodcock broods.

Study Area and Methods

The Baring Unit of the Moosehorn National Wildlife Refuge is located in eastern Washington County, Maine, near the Canadian border. Mendall and Aldous (1943) conducted an early study of woodcock ecology and management on both the Baring and Edmunds units of the refuge. Major cover types on the area range from pure coniferous to pure hardwood, with scattered openings consisting of hayfields, blueberry (*Vaccinium angustifolium*) fields, old homesites, and in recent years small to medium-sized (0.1–8.1 ha) clearcuts. The most common conifers are white pine (*Pinus strobus*), spruce (*Picea* spp.), and balsam fir (*Abies balsamea*), all occurring in both pure and mixed stands. Hardwood species include white birch (*Betula papyrifera*), gray birch (*B. populifolia*), red maple (*Acer rubra*), and aspen (*Populus* spp.). Speckled alder (*Alnus rugosa*) occurs commonly in wet areas and as an invader in old fields.

Woodcock broods were located each year from 1977 to 1980, using techniques described by Ammann (1974, 1977). Briefly, this involved searching all likely areas in forest stands, along upland field edges and roadsides, and in alder covers with one or two trained pointing dogs. The only major cover type not routinely searched consisted of pure spruce–fir stands. When broods were located, a special effort was made to capture the hen as well as to locate and capture all chicks. Brood size was always presumed to be four until very careful searching did not yield four chicks. In fact, most broods of less than four chicks were purposely relocated one or more days later to make sure chicks had not been overlooked. Intensive brood searches usually began about 10 May each year and concluded by 1 June. A few broods were located each year after 1 June, especially in 1980.

The hens and all chicks were banded, weighed to the nearest gram, and bill-length measurements taken to the nearest 0.5 mm. Chicks were aged in days, using bill-length measurements (Ammann 1974), and hens were separated into age classes by wing characteristics (Martin 1964). Hens 1 year old are defined as second year (SY), and hens 2 years old or older are defined as after second year (ASY).

An intensive banding program using ground traps (Liscinsky and Bailey 1955), mist nets (Sheldon 1967), and nightlighting techniques Rieffenberger and Kletzly 1967) was conducted on the study area each year from the first week of June until the last week of August. This trapping program involved daily ground trapping on nine traplines consisting of from 6 to 23 separate traps located in predominately alder covers throughout the study area. Mistnetting was conducted weekly on all major upland fields and forest openings on the study area that had a past history of nocturnal roosting by woodcock. From 10 to 30 nets were used in each field per night, depending upon field size. Nightlighting techniques were used in the same fields when weather conditions were optimal (meaning overcast skies with moderate to heavy rain). These weather conditions normally occurred less than once per week during the 12- to 13-week capture period each summer.

Vegetation data were gathered at brood sites from 1977 to 1979, using the techniques of James and Shugart (1970). This involved measuring all trees and calculating shrub density and canopy height in a 0.04-ha circle centered at each brood capture site. The Statistical Analysis System (SAS) group of computer programs (Barr et al. 1979) was used in data analysis.

Brood Females

Age-Specific Nesting Ecology

Of the 102 brood females, 69 were caught with their broods. The largest percentage of brood hens were ASY females in three of the four years (Table 1). In 1978, however, more than half (58%) of the brood females encountered were SY (Table 1). Total captures of all females each year showed the same relative proportion of ASY and SY females as did captures of only brood females. Thus, more SY females were present in the overall population in 1978 than in the other three years.

The average brood size per ASY hen was larger than the average brood size per SY hen in all years (Table 1). Results of a t-test, however, were not significant ($P > 0.10$), either for any one year or over all years. Each year, peak hatching dates for all broods occurred during the first and second week of May (Fig. 1). Peak hatching date based on our brood searches was somewhat later for broods with SY hens in 1977 and 1979 (Table 1). In 1980, however, the peak hatching date for broods with SY hens was earlier. A much wider range of hatching dates was exhibited by SY brood females than by ASY hens in all years except in 1980.

Table 1. *A yearly comparison of American woodcock brood data from Maine, based on brood female age.*[a]

	Percent brood females		Average brood size per		Peak hatching date for broods	
	ASY	SY	ASY	SY	ASY	SY
1977	75 (15)	25 (5)	3.1	2.7	10 May	15 May
1978	42 (8)	58 (11)	3.5	3.2	12 May	13 May
1979	70 (7)	30 (3)	3.9	3.0	9 May	15 May
1980	75 (15)	25 (5)	2.9	2.8	11 May	7 May
All years	65	35	3.5	2.9	10 May	12 May

[a] Sample size in parentheses.

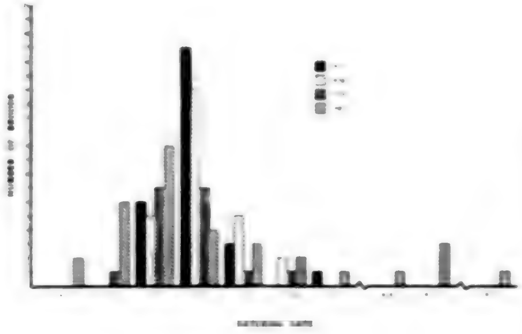

Fig. 1. Hatching chronology of American woodcock broods, 1977–80. Date shown is the midpoint of a 5-day period.

Female Homing

From 20 to 50% of the females captured each year had been banded on the study area in a previous year. Six brood females were recaptured in two of the four years of study. With one exception, capture locations for these females were in the same general area as previous capture sites. The mean distance between capture sites was 303.5 ± 55.8 m (range, 120–600 m). Two of the six recaptured hens were quite old when last contacted (5 and 8 years old).

Five returning brood females had first been banded on the study area as chicks. Two of the five were caught with broods in the same location (± 5 m) where they had first been banded as chicks the previous year. The other three hens were captured from 840 to 1,380 m from their original capture sites.

Chicks

A total of 338 chicks was captured during the four-year study. Recapture rates for chicks during summer trapping operations were 43, 31, 38, and 22% during 1977 to 1980, respectively.

Growth of Woodcock Chicks

Weight data from captured chicks of various ages provide some indirect evidence of the growth rate to slightly beyond flight stage. Since many fledged chicks were recaptured later each summer when they could be sexed, we were able to look at the effects of sex, year, and of hen age on the weight increase (g/day) of chicks.

Table 2. *Linear model, showing the effects of year, chick sex, and hen age on chick weight.*

Source	df	*F*-value	*P* > F
Model	11	131.32	0.0001
Year	3	1.24	0.3039
Chick sex	1	4.68	0.0345
Hen age	1	0.30	0.5865
Brood age	1	849.30	0.0001
Brood age × year	3	0.67	0.5770
Brood age × chick sex	1	6.95	0.0106
Brood age × hen age	1	0.11	0.7445

A linear model (Table 2) showed that chick sex had a significant effect on the growth rate. Females gained weight at a faster rate (P = 0.011) than males (Fig. 2). The growth rate of male chicks was 5.1 g/day, whereas the growth of female chicks was 6.2 g/day. This result was expected, since adult females weigh more than adult males (Mendall and Aldous 1943; Sheldon 1967). Nonetheless, this is a very rapid growth rate for both sexes, and substantial amounts of high-protein foods must be required to sustain it. Sheldon (1967) documented that captive adults need approximately their body weight in earthworms per day to maintain their weight.

We also tested for differences in weight gain of chicks between the two age classes of hens (Table 3). The growth rate of chicks with SY hens was significantly slower (P = 0.013) than that of chicks with ASY hens; this difference amounted to 0.5 g/day.

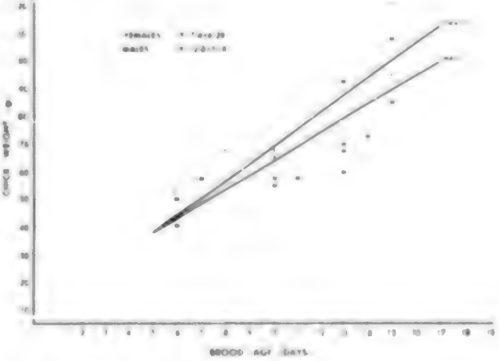

Fig. 2. Weight gain of male and female American woodcock chicks. Each value on the graph may represent more than one observation.

Table 3. *Linear model, showing the effects of hen age on chick weight.*

Source	df	F-value	P > F
Model	3	1498.9	0.0001
Hen age	1	7.6	0.0063
Brood age	1	4083.9	0.0001
Hen age × brood age	1	6.3	0.0126

Table 4. *Percentage of males in recaptures of fledged chicks and the probability of obtaining the observed sex ratio if the real sex ratio was 0.5.*

Year	Number	Percent	Probability
1977	37	51.3	1.000
1978	31	32.2	0.071
1979	23	69.6	0.093
1980	21	57.1	0.664
All years	112	50.9	0.925

Survival of Chicks to Fledging

A good indication of the mortality of chicks to slightly beyond flight stage is available from the 102 broods of various ages captured during the study. A regression model was constructed of the number of chicks per brood versus brood age. An equation of the form $\hat{Y} = -0.09x + 3.9$ resulted, indicating a low attrition rate (0.09 chicks per day) for chicks over the entire brood period. Mendall and Aldous (1943) also concluded that the attrition rate was low in woodcock broods but provided no supporting data.

We also examined our data to see if hen age had any effect on brood size and thus on chick survival. Recall that a previous analysis had shown faster weight gain and a greater average brood size for broods with ASY hens. A linear model that tested the effect of year and hen age on brood size approached significance ($P = 0.08$) for year effects only. Thus, year effects may be more important in determining brood size and chick survival than hen age. It may also be that we could not detect the effect of hen age on survival because of sampling variation. A difference in growth rate of 0.5 g/day due to hen age would seem to have significant survival value.

Sex Ratio of Young

The sex ratio of fledged chicks we recaught later each summer was not 50:50 in all years. A chi-square analysis in a 2 × 4 contingency table showed significant yearly variation in the sex ratio ($X^2 = 7.84$, df = 3, $P = 0.049$). To determine which years explained the variation, we calculated the exact binomial probability (Siegel 1956) of obtaining the observed sex ratio if the real ratio was 50:50 (Table 4). In 1978, the sex ratio was skewed ($P<0.10$) toward females, and in 1979, the reverse was true (Table 4).

Fisher (1930) first hypothesized that if one sex of offspring cost more to produce in terms of parental investment, the sex ratio should be skewed toward the other sex at the time of independence. Howe (1977) presented data on sex-ratio adjustment in the common grackle (*Quiscalus quiscula*), a strongly sexually dimorphic species in which males participate in rearing the altricial young. He argued that since female grackles were smaller, they were the least expensive sex to rear and would be favored during times of resource scarcity. American woodcock also show strong sexual size dimorphism, but in the opposite direction than grackles (i.e females are larger). Young of the American woodcock are precocial, and there is no male parental investment in rearing young (Mendall and Aldous 1943). Female woodcock chicks are larger and they grow more rapidly (Fig. 1) than males, and thus probably cost more to rear in the context of Fisher's (1930) and Howe's (1977) argument. Our data seem to support Howe's (1977) argument, since we have some evidence that 1979 was a year of environmental stress, and the sex ratio from the sample of fledged young favored males. Total precipitation during late April (late incubation period) and during the entire month of May (hatching period) was four times as high (more than 31 cm) as the average for the other three years (Table 5). In fact, overall production of young seemed much lower in 1979, with captures of all chicks down by one-third and overall summer captures of hatching-year birds down 40%.

Precisely how much care a woodcock female affords her precocial young is unknown. Sheldon (1967) believed that American woodcock chicks could feed themselves as soon as the yolk sac was resorbed. Tuck (1972) believed that snipe (*Capella gallinago delicata*) chicks were dependent on an adult for food during the first week or two of life because of their short bills, which

Table 5. *Average daily maximum temperature and total precipitation on the Moosehorn study area during the last week of April and in May, 1977–80.*

Year	Average daily maximum temperature (°C)	Total precipitation (cm)
1977	17	10.8
1978	19	3.9
1979	14	31.2
1980	16	7.8

could not reach the main source of food in the soil. Marcstrom and Sundgren (1977) showed that European woodcock chicks (*Scolopax rusticola*) were not adept at feeding themselves until they were 1 week old. Although we have no data on chick feeding, our experience shows that female woodcock brood their chicks at night and during inclement weather until they are 2 to 3 weeks old. The assumption can logically be made then that female woodcock are very important to the survival of their chicks for a significant part of the brood-rearing period. Because female chicks are larger and grow at a more rapid rate, hens could find it difficult to brood them during their first weeks of life in the event of inclement weather.

Trivers and Willard (1973) argue that species with high variance in male reproductive success (compared to females) should show high variance in sex ratios produced, based on differences in female condition. Male woodcock certainly have high variance in reproductive success because of their polygamous mating system (Sheldon 1967) and the presence of subdominant males at courtship sites (Whitcomb 1974; Godfrey 1975) that may not inseminate any females. We might speculate then that the production of more female young in 1978 was the result of the preponderance of SY brood hens (Table 1), which were in poorer condition than ASY hens. We could not, however, demonstrate any difference in condition between SY and ASY hens by using weight as a criterion. Compared with the other three years, 1978 was the warmest and driest (Table 5). Perhaps these more favorable conditions allowed the production of more female young.

The sex ratio for all years was close to 50:50 (Table 4). Thus, despite yearly variation, the long-term result is production of equal numbers of each sex.

Summer Association of Fledged Chicks

More than one member of the same brood was recaptured in 25 of the 102 broods. In 14 of these broods, two or more members were captured in the same location. Of all recaptured chicks, 57% were contacted on the same trapline or in the same roosting field as a sibling. Horton and Causey (this volume), using radiotelemetry, found that members of the same woodcock brood were found in close association for up to 6 weeks after brood breakup. These results indicate that even after brood breakup, sibling mates maintain a strong attraction to the same covers.

Habitat Selection

Woodcock broods were found in virtually all types of cover on the study area. Predominant tree species at brood sites were gray birch, aspen, spruce, white pine, balsam fir, red maple, and white birch (Table 6). Alder, beaked hazel (*Corylus cornuta*), willow (*Salix* spp.), and Viburnum (*Viburnum* spp.) were the most important shrub species (Table 6). Examination of importance values (Curtis and McIntosh 1951) for major tree species (Table 6) indicates that even though conifers are usually present, two hardwood species (gray birch and aspen) are by far the most important components of the forest stands at brood sites. Coniferous components of forest stands at brood sites were mainly understory species, as indicated by their relatively low importance values.

Habitat Selection Versus Brood Age

Vegetation information from brood sites was examined to determine if vegetation structure was similar at brood sites regardless of the age of the brood. Broods were separated into two groups on the basis of their age: very young broods (1–5 days old), and broods older than 5 days.

Three vegetational variables – stems per hectare of trees 7.6-15.2 cm DBH, total trees per hectare, and total basal area (m^2/ha) – were significantly greater at sites where very young broods were found (Table 7). A correlation matrix of all variables showed a large, significant ($P < 0.0001$) correlation between the first and the second of these variables, indicating that the

Table 6. *Frequency of occurrence (%) of major tree and shrub species at woodcock brood locations in Maine and importance values for major tree species.*

Species	Frequency (%)	Importance value[a]
Trees		
Gray birch (*Betula populifolia*)	85.5	74.2
Aspen (*Populus* spp.)	75.0	70.5
Spruce (*Picea* spp.)	66.0	20.4
White pine (*Pinus strobus*)	54.0	27.8
Balsam fir (*Abies balsamea*)	52.5	19.2
Red maple (*Acer rubrum*)	49.5	31.9
White birch (*Betula papyrifera*)	36.0	23.2
Choke cherry (*Prunus virginiana*)	19.5	3.5
Tamarack (*Larix laricina*)	15.0	9.1
Red pine (*Pinus resinosa*)	10.5	1.8
Wild apple (*Malus pumila*)	6.0	1.0
Pin cherry (*Prunus pennsylvanica*)	4.5	0.9
White ash (*Fraxinus americana*)	4.5	1.1
Black cherry (*Prunus serotina*)	3.0	0.7
American beech (*Fagus grandifolia*)	3.0	1.2
Northern red oak (*Quercus rubra*)	3.0	0.6
Striped maple (*Acer pennsylvanicum*)	1.5	0.5
American elm (*Ulmus americana*)	1.5	0.4
Shrubs		
Speckled alder (*Alnus rugosa*)	58.5	
Beaked hazel (*Corylus cornuta*)	39.0	
Willow (*Salix* spp.)	30.0	
Viburnum (*Viburnum* spp.)	27.0	
Spirea (*Spirea* spp.)	10.5	
Serviceberry (*Amelanchier* spp.)	7.5	

[a] Importance value = sum of relative frequency, relative density, and relative dominance ÷ 3 (Curtis and McIntosh 1951).

Table 7. *Mean and ± SE (given in parentheses) of vegetational variables at capture locations of different-aged woodcock broods.*

	Brood age	
Variable	Very young[a] (N = 23)	Older[b] (N = 42)
Number of trees/ha		
7.6–15.2 cm DBH***	112.2 (10.4)	76.1 (7.7)
15.3–22.9 cm DBH	29.4 (4.5)	26.5 (3.3)
23.0–38.1 cm DBH*	4.6 (2.1)	8.9 (1.5)
38.2–53.3 cm DBH	0.4 (0.2)	0.3 (2.0)
Number of small trees/ha (< 7.6 cm DBH)	248.8 (37.8)	186.9 (27.9)
Shrub stems/ha	11,155.1 (2,811.4)	12,916.6 (2,080.5)
Total trees/ha**	146.7 (12.8)	111.8 (9.5)
Total basal area (m^2/ha)**	12.4 (1.1)	9.1 (0.8)
Canopy height (m)	14.5 (1.0)	13.5 (0.8)

[a] Very young = 1–5 days old.

[b] Older = 5 days old or older.

*$P < 0.10$.

**$P < 0.05$.

***$P < 0.01$.

presence of trees 7.6–15.2 cm DBH was a controlling factor in values for total trees per hectare and total basal area per hectare. The number of stems per hectare of intermediate-sized (22.9–38.1 cm DBH) trees was significantly greater (at the 10% level) at sites where older broods were found (Table 7).

Stepwise discriminant analysis, which develops an equation that maximizes between-group variation (Lachenbruch 1975), was performed on all habitat variables. This analysis indicated a significant ($P < 0.01$) discriminating function which picked one variable (stem density of trees 7.6–15.2 cm DBH) as being the most important in separating the two groups. The classification matrix from the discriminant analysis indicated that 66% of the brood plots could be separated into the two age classes on the basis of only this variable.

Bourgeois (1977) presented evidence of a shift in habitat preference between nest-site locations and sites where broods were found; he reported that brood sites were characterized by a greater basal area and greater density of trees in the intermediate-size class. The shift in habitat structure between areas used by young and older broods seems to indicate that older broods prefer more open (fewer stems per hectare) forest stands of older age classes. Thus, the direction of the habitat shift in both studies is toward areas that are more open and have larger numbers of intermediate-size trees.

Conclusions

The present study has refined our understanding of several factors in the life history of woodcock broods. There appear to be some age-related differences in production by female woodcock that are manifested in smaller brood sizes, later hatching dates, and slower weight gain of chicks for broods from SY hens. These differences may simply be the result of the inexperience of SY hens. However, there is no evidence that chicks with SY brood females survived at a lower rate, at least through the brood-rearing period.

Our evidence for yearly variation in the sex ratio of fledged young woodcock is the first report of a skewed sex ratio in this precocial, polygamous species. It seems likely that sex-ratio adjustment in birds might occur more often in species with no male parental care. A single parent might find it more difficult to care for young during times of environmental stress, and the more expensive sex to rear would be selected against. The effect of unbalanced sex ratios on woodcock populations needs further study.

The finding that broodmates tend to remain in the same covers throughout the summer period has important management implications. Future research that provided information on the amount of land area frequented by locally hatched woodcock could set boundaries on the size of managed habitat units. Owners of small landholdings might be more easily convinced to manage their landholding if they knew that birds they produced would be faithful to their covers throughout the summer and into the fall.

Finally, this study indicates that habitat preference changes during the brood-rearing period toward more open, mature stands with smaller numbers of trees per hectare. To maintain an optimal pattern of habitat diversity for woodcock broods, managers need to take note of this age-specific habitat preference.

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Association Among Woodcock Brood Members After Brood Breakup

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Abstract

Seven broods of American woodcock (*Philohela minor*), including 19 chicks and 5 adult females, were radio-tagged in east-central Alabama in spring 1976 and 1978. The brood-rearing period ranged from 31 to 38 days (average, about 34 days). The association of brood members following brood breakup was determined for four broods. After brood breakup, chicks were more closely associated with other brood members than with adult females. During the first 2 weeks after breakup, close association (< 50 m distance between brood members) occurred primarily in diurnal coverts. After the third week, close association among chicks occurred mostly at night. The final close association among members of two broods occurred during the fifth and sixth weeks after brood breakup (64 and 72 days of age, respectively). This study suggests that most social bonds among members of a woodcock brood are lost by the sixth week following brood breakup.

The duration of brood-rearing period of the American woodcock (*Philohela minor*) varies throughout its traditional breeding range (Sheldon 1967; Wenstrom 1973; Caldwell and Lindzey 1974). This variability is probably influenced by individual brood behavior as well as the judgment of investigators who delimit such things. Some members of the same brood appear to have similar activity patterns for extended periods after formal brood integrity is lost. Pettingill (1936) and Mendall and Aldous (1943) believed young woodcock brood members remained together even after they were fully grown. We have observed groups of two or three woodcock in fields at night and questioned whether these groups represented members of the same brood. We undertook this study to document more fully the association among woodcock brood members following brood breakup in a small sample of broods.

Study Areas

A 143-ha area within Tuskegee National Forest (TNF) in Macon County (located approximately 24 km southwest of Auburn, Alabama) was the primary study area. This area lies within Alabama's Coastal Plain physiographic region with elevations varying between 92 and 131 m ASL (above mean sea level). The study site comprised 34 ha of pine stands ($\bar{x}$ size = 9 ha) between 3 and 8 years of age and 109 ha of forested land. Numerous areas devoid of seedling pines, resulting from burns during the second and third year after establishment, characterized young pine stands. Forested lands consisted of sawtimber size (> 35 years of age) southern pines in upland sites, and mixed stands of pines and hardwoods in bottomlands. One stream, impounded in numerous places by beavers, flowed through the area. Cuthbert sandy loam was the most common upland soil type, and alluvial soils were most common in bottomlands (Lounsbury et al. 1944). The Lee County study area consisted of a 40-ha flood plain along Town Creek in a residential section within the city limits of Auburn, Alabama. Two hectares of kudzu (*Pueraria lobata*) and 38 ha of mixed pines and hardwoods occurred in this area.

Methods

We intensively searched our study areas for woodcock broods using trained pointing dogs during the springs (February–June) of 1976 and 1978. Broods were captured with hand-held nets (Ammann 1974). Adult females were aged by wing characteristics (Martin 1964) and chicks by bill length measurements (Ammann 1974). All birds were banded with U.S. Fish and Wildlife Service leg bands.

Chicks older than 7 days and/or weighing more than 40 g and adult females were fitted with Model SM-1 transmitters ($\bar{x}$ wt = 4.0 g, theoretical life = 120 days) manufactured by AVM Instrument Co., 810 Dennison Drive, Champaign, Illinois 61820, or Model MP-1116-LD transmitters ($\bar{x}$ wt = 4.6 g, theoretical life = 56–75 days) marketed by Wildlife Materials, Inc., R.R. 2, Carbondale, Illinois 62901. A latex harness (Godfrey 1970) was used to attach transmitters to the birds.

Techniques used for locating instrumented birds have been described previously (Horton and Causey 1979). All telemetry data were gathered after brood breakup. We used only "simultaneous" locations of brood members in data analysis. The maximum interval during which we assumed brood-member locations were simultaneous was 10 minutes. Locations of brood members were plotted on maps of the study area at weekly intervals.

The distance separating brood members was measured on maps for each location. Acknowledging the location error discussed by Horton and Causey (1979), we designated a separation distance of <50 m as a "close" association. We judged a separation distance between 50 and 100 m as "relatively close," between 100 and 200 m as "separate," and >200 m as "widely separate."

In this study, several criteria were used to judge whether brood breakup had occurred. These were: (1) use of fields at night, (2) separation of brood members, (3) absence of adult female decoy behavior, and (4) brood members flushed as individuals rather than simultaneously (Caldwell and Lindzey 1974).

Results

Seven woodcock broods including 10 chicks and 5 adult females were radio-tagged in 1976 and 1978. No broods were found on either study area in 1977. Spatial associations of four broods were intensively studied (Table 1). We used data from three broods (I, II, and III) for association between adult females and chicks and from two, 2-chick broods (II and IV) for chick–chick associations.

Table 1. *Composition and monitoring periods for woodcock broods studied in 1976 and 1978, Lee and Macon counties, Alabama.*

Brood no.	Brood composition[a]	Monitoring period (weeks)
I	AHY Hen	1
	Chick 1	1
II	AHY Hen	2
	Chick 1	7
	Chick 2	7
III	SY Hen	1
	Chick 1	1
IV	Chick 1	5
	Chick 2	5

[a] AHY = after hatching year; SY = second year.

Brood Breakup

Use of fields at night, separation of brood members, and absence of female decoy behavior, either singularly or in combination, appeared to be a good indicator of brood breakup. Flushing brood members individually was not a satisfactory criterion, since brood members could be flushed individually when persistent radio-tracking indicated brood integrity had not been lost. The length of the brood-rearing period for the seven broods ranged from 31 to 38 days ($\bar{x}$ = 34 days).

Association of Brood Members After Breakup

During the first two weeks after breakup, 54% of the distances between chick locations (Table 2) were classified as close or relatively close. Most of these close or relatively close associations (45 of 46) occurred in diurnal coverts. Eleven of 12 chick nocturnal locations were classified as separate or widely separate during this same two-week interval. Of the distances separating females and chicks during the first two weeks after breakup, 41% (16 of 39) were classified as close or relatively close. All (4 of 4) nocturnal female-chick locations were widely separated. Adult

Table 2. *Distances separating woodcock brood members grouped by weekly intervals after brood breakup in Lee and Macon counties, Alabama, 1976 and 1978.*

Weeks after brood breakup	Site[a]	Number of locations				
		< 50 m	50-100 m	100-200 m	> 200 m	Total
1	D	19	8	11	9	47
	N	1	0	3	5	9
2	D	8	10	4	5	27
	N	0	0	0	3	3
3	D	0	6	6	4	16
	N	0	3	5	3	11
4	D	0	3	4	11	18
	N	5	3	0	0	8
5	D	1	1	1	10	13
	N	8	0	0	1	9
6	D	0	0	1	8	9
	N	4	0	0	0	4
7	D	0	0	0	6	6
	N	0	0	0	6	6

[a] D = diurnal location; N = nocturnal location.

female–chick separation distance averaged 169 ± 38 m (± SE) for the first week and 179 ± 41 m for the second week. Chick-chick association distances averaged 103 ± 18 m and 100 ± 20 m, respectively, for the same times. Activity patterns of chicks varied during these two weeks and appeared to us to be the final signs of a weakening affinity among brood members.

A gradual shift to new diurnal coverts occurred during the third week, resulting in an increase in the average separation distance between chicks ($\bar{x}$ = 159 ± 32 m). At this time we also observed an upward trend when we regressed separation distances against days after breakup (Fig. 1). During the third week after breakup, three of nine relatively close locations occurred at night. This began a reversal of the trend noted during the first two weeks when most close or relatively close locations occurred in the daytime.

During weeks four through six, 20 of 25 close or relatively close locations were recorded in forest openings at night. During this same period, 24 of 25 separate or widely separate locations were diurnal locations. The distance between chicks from broods II and IV averaged 204 ± 27 m during the fourth week, 314 ± 56 m during the fifth week, and 385 ± 61 m during the sixth week.

The last close association for brood II occurred during the sixth week and during the fifth week for brood IV. Chick age in brood II and brood IV, when the last close contact was recorded, was approximately 72 days and 64 days, respectively. All of the 12 locations recorded during the seventh week following brood breakup were classified as widely separate.

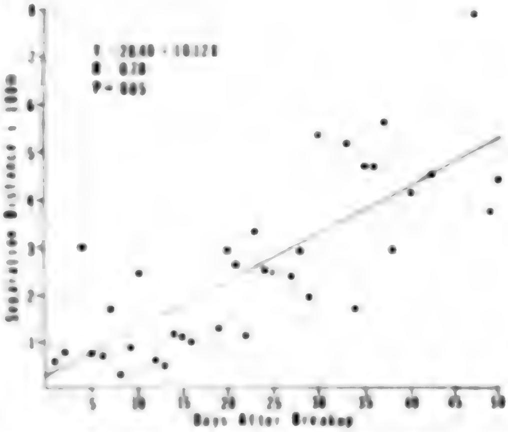

Fig. 1. Relation of the distance between chick brood members to days after brood breakup, Macon and Lee counties, Alabama, 1976 and 1978.

We regressed the separation distances between chicks against days following brood breakup (Fig. 1) and computed a significant linear regression for these data ($P < 0.05$, $r = 0.7768$, df = 34). We also tested for differences between mean distances separating adult females and

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chicks and mean distances between chicks, using an analysis of variance. No significant difference ($P < 0.05$) was calculated because of the short monitoring period for females and the large variability in separation distances recorded during the first two weeks.

Discussion

Based on our criteria, we determined that the broods we studied experienced breakup between 31 and 38 days after hatching. For about two weeks after breakup, chicks apparently undergo a period of adjustment leading ultimately to independent existence. During this time, chick brood members were usually located close to each other during the daytime and far apart at night. The first use of forest openings at night varied among chicks (G. I. Horton and M. K. Causey, unpublished data) and led to separate or widely separate nocturnal locations. Daytime association among chick brood members decreased as chicks grew older, and by the fourth week following breakup, close association was recorded primarily at night. The final close association between chicks occurred during the sixth week after breakup. These data support Pettingill (1936) and Mendall and Aldous (1943), who believed some brood continuity was present even after brood breakup.

G. A. Ammann (personal communication) and Whitcomb (1974) reported that pointing dogs located only about 33% of the woodcock broods in an area even when that area was searched intensively. We have noted a discrepancy between the number of broods found near certain fields and the number of woodcock observed flying to those fields at night after brood breakup (G. I. Horton and M. K. Causey, unpublished data). If, as our limited data indicate, brood members rest in close proximity to each other at night, then researchers might be able to more accurately determine the breeding densities around selected fields by flushing woodcock "groups." Further study is necessary to determine the number of remnant broods that behave as the broods we investigated, the maximum area occupied by a "group" at night, and the correlation between "flushed groups" and the number of broods located by pointing dogs. Although many unanswered questions remain concerning the post-brood-rearing behavior of woodcock chicks, it seems clear that some association among brood members remains for as long as six weeks following brood breakup.

Acknowledgments

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Changing Forest Land Uses and Opportunities for Woodcock Management in New England and the Maritime Provinces

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Abstract

Land-use trends in New England and the Maritime Provinces include continued loss of land to urban uses, decrease in the amount of farmland reverting to forests, greatly intensified forest management of large areas, and expanding public interest and influence in forest land management. Fragmentation of small woodlots has increased the number of urban-oriented owners who seek a variety of amenities from their land; timber management often is not a primary objective. Larger ownerships are commercially oriented, and many new intensive silvicultural practices are being applied to meet rising demands for wood. All of these changes will significantly affect the habitat of woodcock (*Philohela minor*).

Wildlife managers are challenged to use existing educational and financial assistance programs and to participate through regulatory processes at the policy level to influence land uses to benefit wildlife.

The New England-Maritime Provinces region (extending from Connecticut to Cape Breton, Nova Scotia) contains thousands of hectares of abandoned farms and a variety of forest types interspersed with bogs, lakes, and rivers that create habitat attractive to woodcock (*Philohela minor*). Data from Wendt et al. (1979) and J. Tautin (personal communication) indicate average or above breeding densities as well as high interest and hunter success for the region in comparison with other parts of the Atlantic Flyway. However, rapid changes in land use are influencing the amount, quality, and distribution of woodcock habitat. A significant downward trend in the breeding population index within the Atlantic Flyway has been recorded (J. Tautin, personal communication).

The objectives of this paper are to (1) identify trends in land use, with emphasis upon forestry, that may have significant impacts on woodcock habitat; and (2) suggest approaches for wildlife managers to capitalize upon land management activities and trends for the benefit of woodcock. There are some clear limitations to these objectives. Although data about land uses are abundant, projections of future land-use trends vary. Many of the driving forces influencing land use are changing, and forecasts by resource economists and land managers are updated frequently. Further, the effect of even the current changes to land cannot be quantified in terms of woodcock habitat. There is no regionwide inventory of woodcock habitat. Finally, information on which to develop guidelines for certain management practices is not available. However, in planning for the future and for identifying potential action programs, the number of hectares involved are not as important as the trends in land use. Furthermore, we suggest that the first priority should be with the decision processes that guide land-use policies rather than with the details of practices.

Land Use

The region of concern includes about 300,000 km² dominated by forests. Except for Prince Edward Island, from 65 to 90% of each state or province is forested. Spruce–fir (*Picea* spp.–*Abies balsamea*) and northern hardwood forests are extensive in the northern states and Canada. A variety of hardwoods and more scattered stands of conifers are typical in the southern areas.

Although farming is important in scattered small areas, the increasing dominance of the forest and the decreasing extent of land committed to farming highlight the potential importance of forest management to woodcock.

Forestry

The forest resource is essential to the economics of New Brunswick, Nova Scotia, and the northern New England states. Spruce and fir are used for lumber and as the principal fiber for the dominant pulp and paper industry. Hardwoods are used for lumber, pulpwood, and a variety of other wood products. Until the turn of the century, hardwoods were used for heating and cooking, and the resurgence of this source of energy in the more rural areas is substantial. Large areas of forest are harvested annually. For example, we estimate that more than 80,000 ha are cut each year in Nova Scotia and New Brunswick.

Characteristics of Forest Owners

Several trends in the use of the region's forests have important implications with respect to woodcock habitat. Characteristics of land owners, their reasons for owning woodlands, and their views about land and forest management practices are critical to the perpetuation and enhancement of wildlife habitat.

Public ownership is common in Canada, where about 47% of the forest land in New Brunswick and 27% in Nova Scotia are controlled by provincial governments. The government of Nova Scotia has a program to purchase cutover areas, with the overall objective of controlling up to a maximum of one-third of the forest land in the province (Cranmer 1974*a*). Only about 6% of the forest land in New England is publicly owned.

About one-third (4,000,000 ha) of New England's forests are owned by the forest industry. Much of this ownership is in large parcels that are concentrated in northern Maine. More than 20% of the forested land in New Brunswick is in large holdings (>200 ha). In New Brunswick and Nova Scotia, each of several companies own more than 40,000 ha.

Two-thirds or more of the woodlands in New England are in nonindustrial, private (usually individual) ownerships (DeCoster 1981). Almost three-quarters of the forests in Nova Scotia, 44% in New Brunswick, and virtually all of the woodlands in Prince Edward Island are privately owned. Information relating to the size of woodlots and to owner occupations and attitudes varies within the region. However, the trends already well established in the more populated southern areas are similar to those beginning to emerge in the northern areas.

Private ownership of forest land has been fragmenting rapidly. The number of owners in New England has nearly doubled from 260,000 in 1952 to 500,000 today (DeCoster 1981). Cranmer (1974*b*) also has commented on fragmentation of ownership in New Brunswick. Many of the private forest ownerships are small. In Prince Edward Island, almost half the woodlots are less than 12 ha (Cranmer 1974*c*). In New England, excluding Maine, the average ownership is less than 20 ha (Gould and Reidel 1979). Somewhat larger parcels are more common in Maine, New Brunswick, and Nova Scotia. Cranmer (1974*a*) noted that in Nova Scotia, almost half of the total forest products came from properties smaller than 400 ha. In New Brunswick, small woodlot owners (land holdings averaging less than 40 ha) own a third of the total forest area.

In relation to habitat management programs, it is noteworthy that only 5% of the individual owners in New England are farmers (Fig. 1), and they hold only about 13% of the forestland. Professionals, executives, retirees, skilled workers, and others dominate the forest ownership. A similar pattern exists throughout the entire northeastern United States (Kingsley 1979). Cranmer (1974*a*) reported that in Nova Scotia, many of the smaller owners do not depend on their forests for their primary source of livelihood.

Reasons for owning forest land and attitudes about timber harvesting are also noteworthy (Figs. 2, 3). Studies in New England show that a sizeable proportion of the owners do not plan to cut wood in the immediate future. According to Gould and Reidel (1979), as few as 12% of the

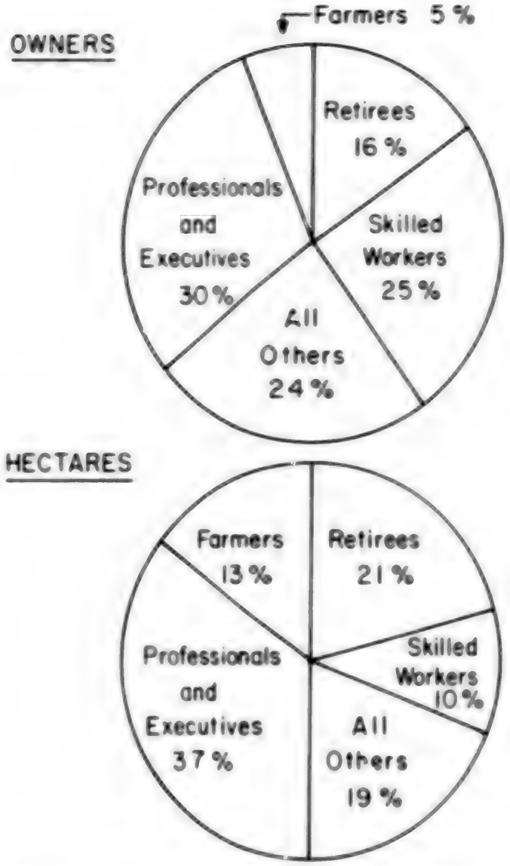

Fig. 1. Classification of forest land owners and the area owned in New England (from DeCoster 1980)

woodlot owners in southern New England have ever harvested trees from their lands.

Many of the private, nonindustrial forest landowners throughout much of the southern part of the region apparently are more interested in amenity value, investment in land, and probably in life-styles associated with rural living than in active forest management activities. A number of owners in New Brunswick place emphasis on their woodlot as something to enjoy for various reasons and chose not to harvest wood for commercial purposes (Tweedale 1974). However, harvesting wood is more common on the private, nonindustrial forest ownerships in the northern parts of the region. In 1974 about $3 million in forest products were sold from Maine farms (Dearborn 1978). For Nova Scotia, Cranmer (1974a) reported that 42 % of the forest products harvested in 1970 came from properties of less than 400 ha.

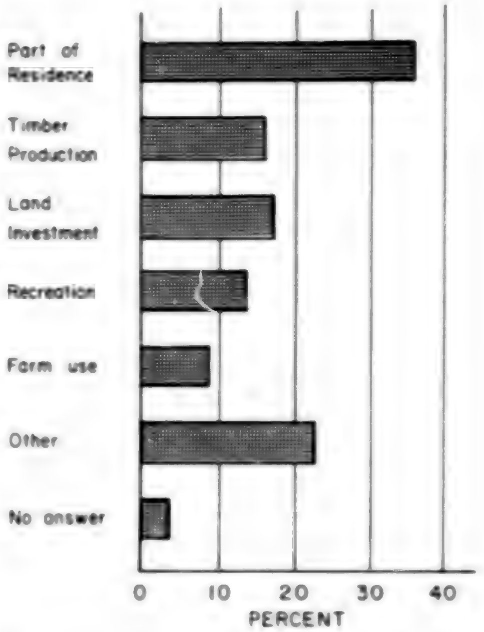

Fig. 2. Percent of land owned by reason for owning (from DeCoster 1980).

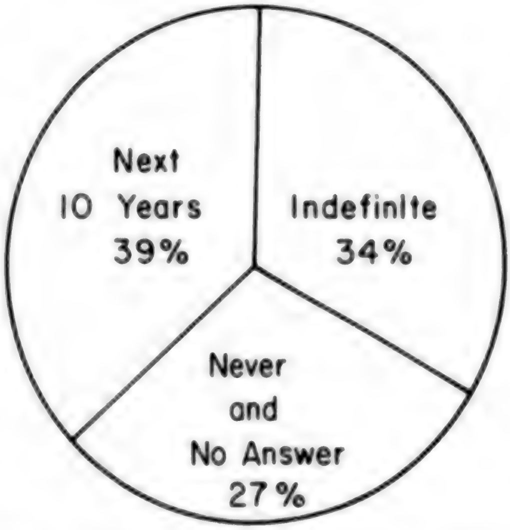

Fig. 3. Owners future harvest intentions by area of forest land for New England, excluding Maine (from DeCoster 1980)

Cutting firewood is a recent major change in the use of small woodlots. New Englanders cut about 3 million cords of firewood for home heating for the winter of 1978–79 (Bailey and Wheeling 1980), a 9 % increase over the previous winter. About 8 million cords are cut annually in New England for lumber, paper, and other products (L. A. DeCoster, personal communication). The recent firewood removals clearly represent a major harvesting activity that can have widespread impacts on forestry as well as on woodcock habitat. We can anticipate increased forestry extension education programs designed to help private woodlot owners practice better forestry through their annual woodcutting operations. Sepik et al. (1977) and Sepik and Dwyer (this volume) have demonstrated the importance of planned cuttings for firewood to woodcock habitat. As suggested by Reeves (1977), the prospect for continued high demand for hardwoods for home fuel offers an excellent opportunity for woodcock habitat management.

Silvicultural Systems and Practices

Although most of the forests in the region have been cut, they have not been managed intensively. Historically, high-quality trees have been removed and inferior trees left. Much of the existing forest is the by-product of opportunistic harvesting that has taken place for more than two centuries. But current and projected demands for wood are causing a major revolution in forest management. More intensive, planned forest management is in progress in the region today than has ever occurred in the past. Intensive management is developing rapidly, especially on the large industrial ownerships and on government-owned areas. This trend offers challenging opportunities for wildlife managers.

Managed forests are treated by one of two major silvicultural systems: even-aged management or uneven-aged management. Both approaches are commonly used throughout the region, but in recent years a trend towards even-aged management has become widespread on some industrial forests in the spruce–fir–northern-hardwood types.

Even-aged management requires removal of most of the trees, usually by clearcutting, sometimes followed by site preparation and planting. The removal of the overstory and disturbance to the site stimulate early seral stages dominated by raspberry (*Rubus* spp.), pin cherry (*Prunus pensylvanica*), aspen (*Populus* spp.), and other pioneer species. Various degrees of clearcutting are practiced. Commercial clearcutting removes only those trees that are economically profitable to harvest. The remaining trees are not cut, and the area is left to regenerate naturally. Complete clearcuts are becoming more common, especially in the northern part of the region. Regeneration may be natural, or the site may be prepared by burning or by mechanical means. Usually a plantation of conifers is established. The new stand may represent a conversion of the site from hardwoods to conifers.

Uneven-aged management usually involves removal of individual trees or small groups of mature trees. Cuts are made over intervals from 10 to 25 years, depending upon site quality and other biological and economic factors. This type of management maintains a continuous forest cover, and the changes in environmental conditions are less drastic.

Each system has advantages and disadvantages from the viewpoint of forest managers. Depending upon the kind of stand and a host of other ecological and economic constraints, some stands are better managed by clearcutting, whereas others respond better to cutting regimes that promote uneven-aged stands. Clearcutting may be dictated by large-scale insect damage or by the maturity of entire stands of trees.

Herbicides may be applied to eliminate vegetation before planting, or to release conifers from competition by overtopping hardwoods. New compounds, improved methods of application, and research about the effects on the plant community are resulting in more selective use of chemicals. Even in hardwoods, all species may not be affected by some herbicides, thus opening new approaches for plant-species management that may have use in both forest and wildlife management. However, public concern about using chemicals in the forest may limit their use.

In Maine in 1978, about 3,200 ha were treated with herbicides (M. L. McCormack, Jr., personal communication). McCormack believes that in the near future as many as 20,000 ha may be treated annually in that State, mostly in small units and chiefly for conifer plantations rather than for stand conversion. Chemicals are routinely used in Christmas-tree management.

Intermediate timber harvests or thinning are done to reduce competition by removing unwanted species and to improve spacing between designated crop trees. Thinning is labor intensive and hence expensive. Some, but not all, thinnings may yield income from trees removed.

The feasibility of using chipped material that is removed during thinnings for pulp or energy is increasing, not only because of changing economics but also because new machinery has been developed. Many small machines for thinning and for woodlot operations have appeared (Young 1980).

If the use of noncommercial species for fuel evolves as a common practice, it will result in cutting on short rotations for biomass. It seems likely that some of the fast-growing pioneer trees such as aspen, birch (*Betula* spp.), alder (*Alnus* spp.) and cherry (*Prunus* spp.) will be exploited through chipping.

A related development is current research with plantations of rapid growing species that are harvested in a few years for fuel or pulp and for other products manufactured from chips. Some of the hybrid poplars (*Populus* spp.), for example, grow several feet each season and produce large tonnages of chips in a few years.

Agriculture

During the late 1800's, all of the region had much more land in agriculture than today. The decline in the number and area of farms during the past 30–40 years has been dramatic (Tables 1, 2). The chief reasons for land being removed from crop production are abandonment of farming and conversion of land to other uses. According to Lapping (1979) and Parks (1977), the rate at which farmland is removed from agricultural production in New England and New Brunswick has been rapid during the recent decades (Fig. 4).

Farmland that has reverted to forest has been the best woodcock habitat in the region. However, much of the earlier reverting land has grown to pole-stage woodlands that are generally of little value to woodcock. Although some land continues to revert, the amount is judged insufficient to counteract lands going out of woodcock production (Owen 1977).

In addition to loss of habitat because of advancing stages of succession, a surprisingly large area is lost annually to other uses. The interim report of the National Agricultural Lands Study (Hidlebaugh 1980) indicates that from 1967 to 1977 in New England, about 90,650 ha per year were converted to urban uses, rural transportation, or impoundments.

Clearly the farm fields that predominated a century ago in many parts of the region have

Table 1. *Decline in number of farms in the Maritime Provinces, 1966–71.*

	Number of census farms[a]		Percent
	1966	1971	decline
New Brunswick	8,706	5,485[b]	35
Nova Scotia	9,621	6,008	37
Prince Edward Island	6,357	4,543	28

[a]Census farm is defined as an agricultural holding of 0.4 ha or more, with annual sales of at least $50.

[b]Dobell (1977) cited unpublished data indicating that in 1976 only 4,551 census farms remained – a loss of almost 50% in 10 years.

Table 2. *Decline in agricultural land in New England, 1949–74.*

	Percent change			Area in
	1949–74	1964–74	1969–74	1974 (ha)
Land in farms	-60.9	-36.6	-12.3	1,984,023
Total cropland	-50.0	-22.1	- 8.2	852,310
Harvested cropland	-48.9	-24.1	- 1.7	580,119

Adapted from Morris (1977).

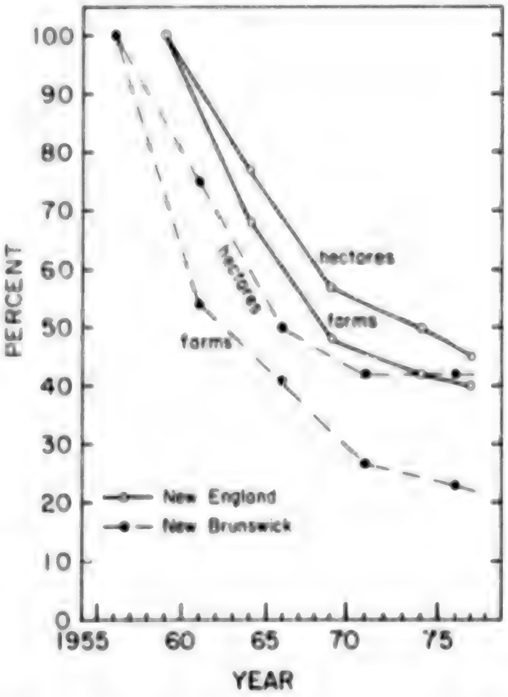

Fig. 4. Percentage decrease in farmlands in New England and New Brunswick since 1955.

been replaced by the small, fragmented woodlots owned chiefly by nonfarmers. Except for the recent increase in firewood cutting, where rural owners are harvesting their own fuelwood, these woodlots for the most part have remained uncut and unmanaged. They are growing out of the stages that are attractive to woodcock.

Trends and Impacts

Several regional trends will have significant impact on woodcock habitat:

(1) *The loss of land to urban uses and developments will continue.* The driving forces for conversion of farmland and forests are rooted in our population patterns and ways of life. Whenever an urban area expands, land almost invariably becomes more valuable for development than for forestry or agriculture. The current major concern for preserving land seems focused on prime agricultural lands. In some New England States, there will be little if any prime farmland remaining by the year 2000 if conversion to nonagricultural uses continues at the present rate (Hidlebaugh 1980). The seriousness of the loss of land other than prime farmlands is not yet receiving widespread attention.

(2) *The amount of land reverting from farming to forest will decrease markedly.* This trend is apparent from the data on farmland that has reverted during recent decades. Comparatively small acreages of farms remain. The energy crisis is stimulating programs to grow more food locally. This factor, coupled with the concern for saving prime agricultural land, will hold current farms as agricultural units.

Abandoned farms have provided some of the best woodcock habitat in the region. A reduction of old farm habitats is occurring and will continue. In view of this trend, intensively managed forests will become increasingly important as future woodcock habitat, as pointed out by Nicholson et al. (1977).

(3) *Much more intensive forest management over larger areas will occur.* Projections about the demand for products show that shortages will occur soon at current rates of growth. Forest management is changing rapidly to meet projected demands. Site preparation, planting genetically superior trees, fertilization, use of herbicides, more complete use of the entire tree, and management concentration on better soils are becoming common practices, especially on the areas of larger ownership in the spruce–fir and northern–hardwood types. One result, important to woodcock habitat and the opportunity for habitat enhancement, is a shift toward shorter cutting cycles and rotations (a cutting cycle is the interval between partial cuts in a stand; rotation refers to the period from regeneration to the harvest of mature trees). Throughout much of the region, rotations of 60–80 years were formerly common, but the intensive forest management now emerging will permit rotations as short as 40 years and cutting cycles of 10 to 15 years in some stands. Frequent cutting in the same stands will create more potential woodcock habitat than long harvesting cycles.

Shorter cutting intervals require road systems that are more extensive and permanent. New, all-season gravel roads on some industrial forests have more than doubled during the past seven years. Forest roads and roadsides are often used by woodcock (Morgenweck 1974; Hale and Gregg 1976; Nicholson et al. 1977). The flexibility of operations is increased by better access, and this new flexibility in management options offers new opportunities to mesh silvicultural activities with wildlife habitat needs.

Products are removed from the forest and stacked, chipped, or loaded at openings created along the road. Such places may serve as singing grounds. Later the sites revert to saplings, providing potential diurnal covers. Reuse of these areas every 10–20 years, setting back the vegetative succession, is beneficial to woodcock.

A negative impact in current trends is the interest in converting hardwood sites to conifers. For woodcock habitat, conifer stands are inferior to hardwoods or mixed stands. Conversion of large blocks to conifers with the consequent reduction of the structural and spatial diversity of forests will necessarily result in poorer woodcock habitats.

The impact of intensive commercial forestry practices on woodcock has not been studied extensively in this region, although Hale and Gregg (1976) documented high use following clearcutting in the aspen-type forests of Wisconsin. The major work that has been reported included combined studies in New Brunswick and Maine (Nicholson et al. 1977). Low densities of birds were found where varying degrees of selective cutting and clearcutting had occurred 1–15 years earlier. The investigators suggested that diurnal habitats resulting from regenerating cutover stands were of poorer quality than those on farmlands and that earthworms were not as abundant or as well distributed on the cutover areas.

Reynolds et al. (1977) have shown that earthworm distribution and abundance are related to previous land use as well as to soil temperature and moisture. Earthworms may occur only at scattered locations within large blocks of spruce-fir and northern hardwoods. Cutting may produce covers structurally acceptable to the birds, but without attractive feeding areas. Since intensive forestry often involves site preparation (which may include mechanical mixing of the organic layer, burning, and fertilization), it would be worthwhile to experiment with establishing earthworms where they are lacking. It seems entirely possible that stocking the best soil sites with earthworms could enhance the attractiveness of surrounding new covers for woodcock. Additional research is needed about this and other aspects of the food base for woodcock in the various types of forest.

The impact of any forest practice on woodcock habitat will vary among forest types and areas. Different responses will also result from varying the spatial and temporal distribution of harvested stands and the kind of site preparation or cultural treatments applied later.

We asked 10 experienced biologists throughout the region to rate the probable impact of a variety of forest practices with a plus–minus scoring system. The forest practices generally rated favorable to woodcock included clearcuts, natural regeneration, use of large machinery, increased forest roads, and site preparation. Land-use trends considered favorable were shorter rotation ages, increased use of firewood, and more use of forest biomass for industrial fuel. Practices generally considered negative were planting (usually to conifers) and conifer release with herbicides. Thinning and selective cutting were seldom considered beneficial, since the changes in the forest stand created by these practices often were not sufficient to alter stand structure significantly for woodcock.

Regardless of the impact of any single treatment at a particular site or forest type, two conclusions seem justified. First, most operations in large areas of unbroken forests will provide new habitats for at least low densities of woodcock. Second, the impact of forestry upon woodcock can be improved by working closely with foresters. Modifications of forest practices need to be applied on a local basis.

(4) *Public interest and influence in land management will intensify.* Public interest in the use of land has become a significant factor in land management. A predominately urban population has become concerned about natural resources. As pointed out by Vaux (1980), "During the last 15 years the reality of these urban values as a dominant part of the forestry situation has been demonstrated in many pieces of forestry-related legislation: national and state environmental quality laws, expanded public programs for forest recreation and wilderness, ..." Further insight about public views is shown by studies indicating that 76% of the respondents to a questionnaire agreed that cutting forests should be done in ways that help wildlife, even if this results in higher prices for wood products (Kellert 1979). Vaux (1980) believes that continued growth of the urban influence appears inevitable.

The ability to recognize the increasing public interest, understand what is being sought and why, and learn how to capitalize on the positive aspects and to cope with those that may be counterproductive is as vital to wildlife biologists as to other land managers.

Recommendations

The trends evident today pose many opportunities and challenges to those interested in wildlife habitat. The constant loss of land to urbanization, increasing numbers of urban-oriented woodland owners, escalating demands for wood, the application of intensive silvicultural techniques new to our region, greater public influence through regulation of land uses – all are developments and trends that will affect woodcock habitat.

Our second objective was to recommend ways for people interested in wildlife (woodcock) to help reduce negative impacts and capitalize on the trends that can have a positive influence on habitat. We have concentrated on approaches to deliver habitat management information to landowners and land managers, rather than on the methods for manipulating habitats. Such methods are best approached locally rather than regionally. Furthermore, although more research is always needed, any competent biologist can detail more management techniques than have ever been applied. *We submit that the current top priority is to become more broadly involved in all land-use activities and to make a planned effort to reach landowners.* Most States and Provinces have indicated a need for habitat management (Owen 1977), but because of the cost, large-scale management is not anticipated. We believe that potentially effective measures are available that will be less costly and more feasible than habitat manipulation programs administered by large agencies.

We discuss four recommendations to enhance woodcock habitat:

(1) *Delivery of habitat management information and philosophy to landowners.* It is convenient to think about this process by separating industrial and large public forests from the small holdings of individual woodlot owners. The larger holdings offer unique advantages. Government and industry have a long-term interest in maintaining productive forests. Either as a result of assigned responsibility, regulatory controls, or corporate policy, the demand for wildlife and the habitat needs of the various species influence land-management decisions on these larger holdings. There are relatively few people to deal with in these areas, yet they are responsible for vast acreages. To meet their needs, they have developed strategic and operational management plans. Soils information, stand inventories, and data on forest dynamics provide the basis for operational cutting schedules and postcutting treatments. The existence and periodic review of these plans give the biologist information to work with and a mechanism for participation. Clearcutting is a commonly used method for harvesting, and we believe that clearcutting has much potential for managing forests for wildlife.

The large size of ownerships allows for flexibility in such matters as the spatial distribution of cuts. Although all the techniques associated with increased use and intensive forest management may not be wholly compatible with woodcock habitat management, there are substantial advantages associated with shorter cut cycles, rotations, and established road systems. Biologists should work with governmental and industrial foresters to take full advantage of these possibilities.

Small ownerships also offer excellent management possibilities, but because of the numbers, characteristics, and diversity of owners, they may be more difficult to reach. The numbers are so large that the few wildlife biologists available cannot accomplish much by direct contact. By working with provincial or state foresters, extension personnel, and others trained in delivering technology to the public, we can benefit from the multiplier effect.

Small landowners may have a mixed set of objectives. Timber management may be a relatively minor goal. More expertise in extension education may be needed to enable us to work with these owners effectively. Our best role may thus be to provide carefully designed workshops, demonstrations, and written guides for delivery to holders of small properties by resource personnel already skilled in working with these people. Our inquiries among service or extension personnel suggest that many of them would welcome workshops, demonstrations, and guides relating to wildlife in the areas they serve.

Furthermore, a surprising variety of landowner forestry assistance programs are active, and wildlife management is a stated consideration in most of them. Some programs have cash incentives for carrying out approved practices. The Federal–Provincial Development Project in New Brunswick assists owners with forest stand improvements, woodlot roads, and other practices. In addition, the program offers field demonstrations and courses available on request by landowners. Similar programs in the United States are administered cooperatively by the states and the U.S. Department of Agriculture.

A recent incentive program is the New England Pilot Fuelwood Project, administered jointly by the Agricultural Stabilization and Conservation Service, U.S. Forest Service, and the appropriate State agencies. The purpose of the program is to promote improved forest management on better sites; wildlife is mentioned as one consideration.

Forest technicians have been hired by some States to work with woodlot owners on the fuelwood project. In some other places, the State service or county forester performs that important function, and consulting foresters in a few areas provide the practical expertise needed. With the anticipated increases in fuelwood demand, a program that offers landowners cash for practicing good management while cutting firewood can offer another very promising way to transmit wildlife information.

Other programs relate to special groups. The forest industry has technical assistance programs for small landowners. Industry foresters prepare management plans for small woodlots and suggest guidelines for harvesting products. Such arrangements are particularly attractive to busy, urban-oriented rural residents or to nonresident owners. Plans are tailored to the goals of individual owners and, with this group, the goals often encompass an interest in wildlife.

The Tree Farm Program, administered by the American Forest Institute, includes 3,411 nonindustrial forest ownerships in New England totaling 2.3 million hectares. In the States from Delaware to Michigan, there are more than 13,500 tree farms (Anon. 1979). This tree farm program encourages management for wood, wildlife, watershed protection, and recreation.

All such programs offer ready-made avenues for the delivery of habitat information. We know that there is some contact by wildlife biologists with these groups. However, nowhere do we have any indication that there is frequent contact, sufficient workshops, or enough pamphlets and guides designed to meet the needs throughout the region that are readily available and easy to use.

(2) *Active participation in decision-level processes.* Opportunities occur daily to influence legislative processes, become involved with other agency planning processes, help set agency priorities, and make recommendations or provide data to land-use planning groups. Biologists can provide factual evidence on the significance of various decisions to wildlife. Data that demonstrate the effect of policy on wildlife goals are the most useful in this context.

An example of a recent opportunity is Public Law 95-306, the Renewable Resources Extension Act of 1978. The act provides for greatly expanded and comprehensive educational programs on renewable resources in the United States, to be conducted through the U.S. Department of Agriculture cooperative extension service with state agency participation; wildlife is included. Although the program has now been authorized, the $15 million needed to carry it out have not yet been appropriated. Funding would add badly needed extension specialists in forestry and wildlife – the very kind of people needed to help transmit habitat management guidelines to and interpret them for small landowners. Although several agencies and organizations worked to develop and pass the legislation, the total thrust by resource people was inadequate to stimulate funding. At one planning meeting to which each State fish and wildlife agency was asked to send a representative, less than 25% did so.

(3) *Active participation in the land regulatory process.* Greater public involvement in land uses, noted earlier, will result in additional regulations. The regulatory process can be helpful in enhancing habitat, but it can also be counterproductive. Thus, constant involvement is needed in all aspects of the process from public hearings for reviewing standards, to routine processes for permit review.

Some of the existing and evolving regulatory programs offer very powerful mechanisms for introducing sensible guidelines to land-management activities. One example is the Crown Lands and Forest Act in New Brunswick that was recently passed by the provincial legislature. The act requires that an industry seeking a license to harvest wood on Crown lands submit a series of management and operational plans for approval. The forestry management plan specifically includes wildlife. How well standards for wildlife are defined and applied in major blocks of forests in New Brunswick will depend, in part, on how well biologists can articulate the details at policy levels. Similar opportunities by one route or another exist in every State and Province.

Habitat is often lost in small pieces. The cumulative effect may be serious, although each individual case may seem insignificant. For example, Mann (1979), reviewed permits issued in response to applications for developments under the Maine site selection law. Each application had been reviewed by State agencies, including fisheries and wildlife, before it was acted upon by the review board. The information recorded for wildlife was used to estimate loss of habitat. As used in her report, wildlife referred primarily to white-tailed deer (*Odocoileus virginianus*), ruffed grouse (*Bonasa umbellus*), and woodcock.

The study revealed that during a 9-year period, new developments in a single county totaled 44.5 km^2. About half, or 22 km^2, was estimated to be wildlife habitat. Results from the study became front-page news locally and were highlighted on prime-time TV and in radio newscasts. The environmental regulatory agency concerned has been discussing plans for an expanded follow-up study. Seminars about wildlife habitat were scheduled for the board members, who make final decisions on project approval.

The study highlighted the cumulative effect of habitat loss. Without question, one small-scale study to quantify a situation we see daily has had a major influence in developing local awareness of a problem. Wildlife habitat should benefit as a result.

(4) *Application of management research to forest lands*. Experimental habitat management has already been undertaken at the Moosehorn National Wildlife Refuge and elsewhere (Mendall and Aldous 1943; Liscinsky 1972; Clark 1973; Hale and Gregg 1976; Sepik et al. 1977; Sepik and Dwyer, this volume). That kind of research should continue in several places to focus on local opportunities as well as to develop techniques that keep abreast of changing forestry practices.

A major need is to test the results from experimental management on small woodlots and large blocks of land. Applications have not been widespread, but are crucial to prescribing recommendations that are practical. Experimental areas can be valuable as demonstration sites. Managed units in major cover types scattered throughout the region should be especially helpful in reaching the logger or woodlot owner.

As a group, wildlife biologists have long espoused habitat management. Progress in applying management techniques to private lands has been very slow for a variety of reasons. Intensive forest management, landowner assistance programs, and changing public attitudes combine to create better opportunities now than previously existed for carrying out wildlife (woodcock) habitat management.

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Relationships Between Land Use and Woodcock Habitat in Pennsylvania, with Guidelines for Rangewide Research[1]

by

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Abstract

An apparent decline in the breeding population of woodcock (*Philohela minor*) in Pennsylvania since 1967 triggered interest in identifying possible factors influencing woodcock numbers in the state. Changing patterns of land use were suspected of playing a major role; consequently, trends in the major categories of land in Pennsylvania were examined to determine possible relations between land use and woodcock populations and their habitats. Land-use data published by the U.S. Soil Conservation Service and the U.S. Forest Service during the mid-1960's and the late 1970's were compared. Pastureland, sapling-seedling stands, and nonstocked forest areas (potentially useful to woodcock) have declined during this period, whereas sawtimber, as well as urban and built-up areas (generally not suitable to woodcock) have increased since the mid-1960's. These trends in land use are consistent with the downward trend in Pennsylvania's breeding woodcock population during the same time. Based on expected socioeconomic developments, projections of land use in Pennsylvania during the next 10 to 20 years were made. Cropland and pastureland acreages are not expected to change much, whereas forestlands are predicted to decline, and urban and built-up lands are expected to increase. In general, the future of woodcock habitat in the state does not appear to be promising. Shortcomings in the existing data base are recognized, and a framework for future research to fill these voids is proposed. The framework consists of an integrated and ordered set of procedures representing a consolidation of earlier research recommendations.

In recent years there has been a downward trend in the breeding population index for woodcock (*Philohela minor*) in Pennsylvania – a decline that prompts concern for the welfare of this species in the State. Among the many factors that may contribute to fluctuations in a wildlife population, availability of habitat is critical to populations of American woodcock (Owen 1977:166). Woodcock require several different kinds of habitat during their annual cycle. On the breeding grounds alone, biologists distinguish among singing, roosting, diurnal, nesting, and brood-rearing habitat. Shortage of any one type of habitat may limit the density or productivity (or both) of breeding populations. The quantity and quality of wintering habitat, and of stopover habitats for migrating birds, undoubtedly also influence the abundance of woodcock throughout their range.

For any game species, the influence of hunting, disease, parasites, and other factors on populations should not be overlooked. For example, there is some evidence that heavy hunting pressure can have a severe impact on local woodcock populations. Liscinsky (1972:48–49) showed that

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the curtailment of hunting in heavily exploited covers can result in increased numbers of breeding birds in spring and larger populations before the hunting season. The question of the role of such factors in the regional abundance of woodcock deserves further attention, but will not be addressed here.

The purpose of the present paper is to examine possible relations between land use and woodcock populations and their habitats in Pennsylvania. To accomplish this, we: (1) present available data on changes in the abundance of woodcock in the State, (2) examine trends in land-use categories potentially beneficial or detrimental to woodcock, and (3) make predictions concerning land-use trends and speculate about their influence on the future availability of woodcock habitat. We also present a general framework for future research.

Woodcock Production and Harvest Trends

Singing-Ground Survey

The number of woodcock counted during the annual spring singing-ground survey in Pennsylvania has declined sharply since 1967 (Fig. 1), the year when singing-ground surveys were first conducted on random routes. Although the interpretation of the singing-ground index is open to question, the survey is the best available measure of the size of woodcock breeding populations. In Pennsylvania, the index has declined at an average annual rate of 7–8% since 1967, whereas the index for the Eastern Region as a whole decreased only 2–3% per year during the same period.

Woodcock Harvests

Since 1971, woodcock harvests in Pennsylvania have been estimated from responses to the annual small-game harvest survey (Shope and McCauley 1974; W. H. Shope 1979, personal communication). This is a questionnaire survey of randomly selected hunters. Harvests are calculated by multiplying the average harvest per licensed hunter by the number of licenses sold.

Except for an unusually high estimate for 1971, annual woodcock harvests in Pennsylvania have remained stable at about 200,000–250,000 birds (Table 1). Because the total annual harvest includes an unknown number of migrant birds originating outside the State, harvests were also calculated for the first 7 days of the open season in each year. Hunting pressure early in the season would likely be concentrated on birds produced within the State, so that any trends in these early harvests might reflect changes in the size of Pennsylvania's breeding woodcock population.

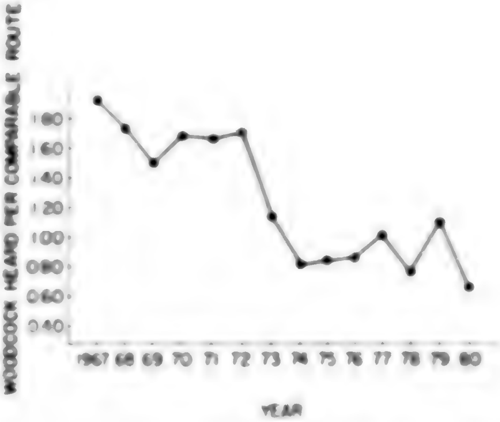

Fig. 1. Trend in number of singing male woodcock in Pennsylvania as determined from annual singing-ground surveys coordinated by the U.S. Fish and Wildlife Service. Estimates were calculated by applying the annual percentage change in the index to data for the base year, 1970.

The number of woodcock harvested during the first 7 days of the season was calculated by applying the percentage of the harvest occurring in the first week (obtained from the U.S. Fish and Wildlife Service woodcock wing-collection survey) to the estimated harvest derived from the State small-game harvest survey. There is no discernible trend in the opening week's woodcock harvest from 1971 to 1979 (Table 1). It is likely that the early harvest has fluctuated according to the timing of the season's opening date in relation to the onset of migration in each year.

Hunter Success

In Pennsylvania, the regular hunting license allows the hunter to take a variety of game. Thus, there are no exact figures on the number of hunters who sought woodcock in each year. As part of the small-game harvest survey, the number of woodcock hunters in the State was estimated for 4 years: 1971, 1973, 1974, and 1979

Table 1. *Woodcock harvests, number of hunters, and hunter success in Pennsylvania from 1971 to 1979.*

Year	Woodcock harvest		Harvest licenses sold	Estimated no. of woodcock hunters	Harvest per licensed hunter		Harvest per woodcock hunter	
	First week	Season total			First week	Season total	First week	Season total
1971	96,482	357,341	1,137,269	147,844	0.085	0.31	0.65	2.42
1972	84,114	210,284	1,139,605	–	0.074	0.18	–	–
1973	83,318	260,369	1,184,975	120,867	0.070	0.22	0.69	2.15
1974	32,822	193,073	1,242,962	105,758	0.026	0.16	0.31	1.83
1975	58,487	224,951	1,280,023	–	0.046	0.18	–	–
1976	107,320	228,341	1,279,925	–	0.084	0.18	–	–
1977	105,854	211,708	1,285,013	–	0.082	0.16	–	–
1978	60,300	201,000	1,275,104	–	0.047	0.16	–	–
1979	78,097	244,054	1,260,742	213,116	0.062	0.19	0.37	1.15

(W. H. Shope, personal communication). Total license sales and estimated numbers of woodcock hunters are presented in Table 1.

One index to the size of a game population is the number of animals harvested per unit of hunting effort, also known as hunter success. By using the number of regular hunting licenses sold (or estimates of the number of woodcock hunters) as an index to hunting effort, we calculated hunter success for each hunting season as a whole, and for the first 7 days of the open season (Table 1). In each case, the number of woodcock harvested per hunting license sold shows little evidence of a trend. However, the woodcock harvest per woodcock hunter has generally declined during the last decade. If the number of hunters is a valid measure of hunting effort, increasing effort should result in a larger percentage of the population being killed. The fact that an increasing number of hunters is harvesting a constant number of birds indicates that the size of the population may be decreasing. Thus hunter success, particularly for the first week of the open season, may indicate a decline in Pennsylvania's breeding woodcock population, supporting the evidence from the annual singing-ground survey. However, it is also possible that woodcock populations have remained stable and that hunter success has declined because of an increasing number of inexperienced woodcock hunters. Clearly, more accurate information concerning the number of woodcock hunters, their skill, the effort they expend, and their success is needed before the true meaning of these hunter-success figures can be determined.

Land-use Trends

In view of the apparent decline in woodcock numbers and the importance of habitat to woodcock populations, our next objective is to examine land-use trends in Pennsylvania and consider the probable impact of these changes on the availability of woodcock habitat (see *Definitions of land-use categories*). In effect, this represents a macro-planning effort in wildlife management, with the life cycle of the species identified in terms of habitat needs and the relative availability of these habitats evaluated over time. An ultimate goal is to determine which habitats may be in critical shortage, and to propose ways of offsetting these shortages. Granted, such a procedure should also consider the carrying capacity of a given habitat and the spatial proximity of various habitats at a local or regional level. However, before involving these more elaborate details, the basics of land-use change must first be examined.

Sources of Data

Two problems were encountered in the study of land use—securing reliable sources of data over time and obtaining data with sufficient detail to relate to the specific habitat needs of woodcock. Information from three sources was reviewed for this study: the U.S. Department of Commerce, Bureau of Census and the U.S. Department of Agriculture, Soil Conservation and Forest Services.

Definitions of land-use categories.[a]

Category	Definition
Cropland	Land used for the production of adapted crops for harvest, alone or in rotation with grasses and legumes, and includes row crops, small grain crops, hay crops, nursery crops, orchard crops, and other similar specialty crops.
Pastureland	Land used primarily for production of adapted, introduced forage plants for animal grazing.
Urban and built-up	Land used for residences, industrial sites, commercial sites, construction sites, institutional sites, public administrative sites, railroad yards, cemeteries, airports, golf courses, sanitary landfills, sewage treatment plants, water control structures, and spillways.
Other land	Farmsteads, farm roads, ditch banks, rural nonfarm residences, investment tracts, strip mines, borrow and gravel pits and idle, open, rural nonfarm land.
Forest land	Land stocked by forest trees of any size, or formerly having had such tree cover, and not currently developed for nonforest use. The minimum area for classification of forest land is 0.4 ha and must be at least 30.5 m wide.
Sawtimber	Land at least 10% stocked with live trees, with half or more of such stocking in trees ≥ 27.9 cm DBH.
Poletimber	Land at least 10% stocked with live trees, with half or more of such stocking in trees ≥ 12.7 cm DBH and < 27.9 cm DBH.
Sapling-seedling stands	Areas at least 10% stocked with live trees, with half or more of such stocking in trees < 12.7 cm DBH.
Nonstocked forest areas	Lands that are less than 10% stocked with live trees.

[a] Obtained from Considine and Powell (1980) and Soil Conservation Service (1980*a*,*b*).

Major differences in acreage totals were noted among the three sources for similar land-use categories and points in time. The differences were due, in part, to the definitions used by the agencies in identifying particular land uses. The Soil Conservation Service (SCS) classifies land on the basis of its "dominant" or "best" use, whereas the Forest Service (FS) considers certain physical features of the land. Land grazed by animals, even if forested, would be classed as pastureland by SCS, on the assumption that this was the land's best use. The same area, however, even if only partly forested, would be classed as forestland by the FS.

Another source of difference among the three agencies originates from their data-collection and sampling procedures. Much of the information developed by the Bureau of Census (BC) comes from the voluntary census of private landowners. The other two agencies conduct on-site evaluations at permanent sample plots, with their overall effort organized by way of statistical designs. The land-use data from the SCS and the FS were therefore considered to be more reliable than those from the BC.

For the purposes of this study, a combination of SCS and FS land-use data was employed. This amalgamation involved the 1965 (Ferguson 1968) and 1978 (Considine and Powell 1980) FS surveys of Pennsylvania and the 1967 and 1977 SCS conservation inventories of Pennsylvania (Soil Conservation Service 1980*a*). Two time points were used for comparison of land-use data: the mid-1960's (1965–67) and the late 1970's (1977–78). Definitions are provided (see box) for the land-use categories that are discussed in the following sections.

Recent Land-use Trends

The basic shift in land use from the mid-1960's to the late 1970's was an increase in urban and developed areas and "other land" (areas with low agricultural value) at the expense of crop, pasture, and forestlands (Table 2).

Two forces were behind these shifts – a continued expansion of metropolitan centers and their arteries, and an economic withdrawal of marginal lands from agricultural production.

Table 2. *Pennsylvania land-use (thousands of hectares; percentages given in parentheses) changes during two inventory periods (1965–67, 1977–78)*[a] *and a comparison of the trends.*[b]

Inventory period	Cropland	Pastureland	Forestland	Urban and built-up	Other land
1965-67	2,503.0 (22)	651.5 (6)	6,636.9 (58)	961.6 (8)	619.6 (5)
1977-78	2,290.9 (20)	503.4 (4)	6,360.9 (56)	1,471.1 (13)	746.3 (7)
Change	-212.1 (-8)	-148.1 (-23)	-276.0 (-4)	+ 509.5 (+ 53)	+ 126.7 (+ 20)

[a] Based on land-use data from Ferguson (1968), Considine and Powell (1980), and Soil Conservation Service (1980*a*)

[b] Total area (11,372,600 ha) surveyed did not change between the first and second inventories.

Urban and Built-up Areas

Pennsylvania experienced a unique demographic situation over this past decade by registering a modest decline in population. During the same period, intensive use of land in terms of urban and built-up usages increased by more than 50%. Basically, a nearly constant population took advantage of comparatively cheap land and cheap energy to satisfy increasing spatial needs. In short, urban sprawl was affordable.

Cropland and Pastureland

The largest loss of farm acreage has been in the southeast portion of the State, where industrial, commercial, and residential interests have outbid farming interests for the basic land resource. This form of land competition was also evident in other urban centers within the State.

Strip or open-pit mining caused further inroads in farm acreage, particularly in western Pennsylvania. Although more stringent regulations now mandate the return of mined lands to nearly their original condition, these areas are removed from agricultural or forest production for considerable lengths of time.

Pennsylvania's agricultural sector has been subject to an attrition of small marginal farms. Such acreage has either been absorbed by larger farm units or diverted to alternate land uses. In particular, Bills and Gingrich (1980) noted a substantial reversion of abandoned farm acreage to forest. A certain portion of this idle farm acreage was subsequently classified as "other land." These areas with low agricultural value and receiving only intermittent use increased 20% from the mid-1960's to the late 1970's.

Initially, this transfer of land out of agriculture was prompted by poorer classes of soil becoming uneconomical to manage for agricultural pursuits. Secondary losses followed as the remaining farm sector fell below a critical mass essential to the maintenance of allied service trades. Insufficient business among farm equipment suppliers and processing and marketing firms resulted in their loss to farm communities; these losses imposed added cost handicaps and secondary reductions to farm operations.

As with croplands, a net loss was realized in pasturelands, again due to the combination of urban encroachment, mining, and financial problems within the livestock industry. During this period, a substantial transfer of pasturage to forest cover occurred in the north-central region. In addition, a shift from pasture to croplands was noted by the SCS in the southeastern agricultural districts. This latter shift was prompted by higher grain and crop prices.

Some increases in pastureland occurred in the Indiana County region (west-central Pennsylvania) from an expansion of dairying and, in the southeastern counties, from a larger number of beef operations. To date, however, beef production in Pennsylvania has been rather static. Statewide, the size of herds has been fairly constant, with some decrease noted over the last few years (Pennsylvania Crop Reporting Service 1980). One of the basic problems confronting Pennsylvania beef producers has been the inability to match rising costs of production with better beef prices.

Forestland

The inroads on forested acreage are largely due to urbanization and, in western Pennsylvania, to strip mining. In addition, a limited conversion of forest to farm acreage has occurred in areas with more productive soil types.

The growth of Pennsylvania's forests over the

Table 3. *Area (in thousands of hectares) of commercial forestland in Pennsylvania by stand-size class, 1965 and 1978.*[a]

	Year	
Stand-size class	1965	1978
Sawtimber	2,967.2	3,086.2
Poletimber	2,354.1	2,026.7
Sapling–seedling	1,315.7	1,248.1
Nonstocked areas	128.7	83.4

[a]Based on data from Ferguson (1968) and Considine and Powell (1980).

past 15 years, in terms of stand size, may be seen in Table 3. A net gain was registered in the acreage of mature sawtimber stands. As poletimber matured to the sawtimber stage, this gain in acreage exceeded the loss from timber harvests and attrition to other land uses. Net losses were recorded in the other three classes, as a measure both of their maturation to larger sizes and of losses to other land uses.

Predicted Land-use Trends

What further changes in land use might be anticipated for the State over the next 10 to 20 years? Energy costs and population increase are two central factors affecting land use; these forces will counter one another during the next 20 years.

Urban and Built-up Areas

A resurgence of growth can be anticipated in Pennsylvania's urban production centers as the U.S. economy returns to its former stature in domestic and world trade. This growth will be tied to a reinvestment in existing industrial centers. Additional nodes of economic growth can be anticipated as allied industries locate adjacent to the current centers and to major eastern markets. A gradual increase in urban and suburban populations will follow.

This period of growth, however, will be tempered by rising costs of energy and, to a lesser extent, of land. Expansions will depend more on reuse or renewal of existing urban and suburban areas. This reinvestment in existing built-up areas will force a more concentrated use of such areas. Housing, transportation, and other social amenities will be directed to more energy-efficient designs, involving less spatial expansion. Although these expansions will be tempered, a net increase in urban acreage can still be expected over the next 20 years. Given that 0.5 million hectares were required in new urban usages during the past span of less than 15 years, the next 20 years will require an addition of at least 0.4 to 0.6 million hectares.

Cropland and Pastureland

Farming should increase in economic stature as our nation continues its role in the world trade of agricultural commodities. A secondary emphasis on instate production will also result as transportation costs force a greater reliance on local sources of foodstuffs. This combination of demands will strengthen the economic structure of the farm sector and promote an increase in cropland and pastureland. In particular, greater attention will be placed on "domestic" production of red meat. Increased pasturage may be garnered from fallow agricultural acreage or "other land" and from partly forested areas. However, the net change to cropland and pastureland over the next 20 years may be negligible, representing a balance between losses to urbanization and gains from marginal farm and forest acreage.

Forest Land

The forested areas of Pennsylvania will also see an increase in economic activity through the harvest of mature stands. A projected increase in the value of the better grade of hardwoods should provide a sufficient inducement for most landowners to realize the economic potential of their resource base. These harvests can be made in a prudent fashion that does not conflict with other amenity values. By the turn of the century, some 1.2 to 1.6 million hectares will have been harvested, with most regenerated into sapling–seedling stands. The net balance in sapling–seedling stands will be nearly 2 million hectares. Poletimber should change to nearly 1.6 million hectares, and sawtimber stands to 2 million hectares. A reduction will also be evident in nonstocked forest areas; basically, our society will not be able to afford the luxury of idle land resources. Overall, by the year 2000, total forested acreage will probably decline to 5.7 million hectares.

Our shift to coal as the key domestic energy source will expand the volume of land affected by strip mining. Most of this will be withdrawn from forested acreage. However, the acceleration of mining will place increased attention on the success of returning mined areas to some logical, alternative land use.

To summarize, there has been a decline in cropland and pastureland in Pennsylvania during the past 15 years. There has also been a decrease in the various stand-size classes of forest land, with the exception of sawtimber, which increased. Other land increased 20%, and urban and built-up areas increased by more than 50%.

We predict that the amount of cropland and pastureland will not change much during the next 10 to 20 years. Forest acreage is expected to decline, except for sapling–seedling stands, which are predicted to increase. Finally, other land may decline, whereas urban and built-up land will continue to increase at a controlled, but noticeable, rate.

But how do these land-use trends relate to the current status and future of woodcock habitat in Pennsylvania? In addressing this question, we first identify the woodcock's major habitat needs during its stay in Pennsylvania and indicate how these needs relate to the land-use categories just examined.

Woodcock Habitat Needs as Related to Land Use

Habitat Needs

Male woodcock in Pennsylvania use a variety of openings to perform their courtship displays, but old fields, pasture, and brushland are used most extensively (Norris et al. 1940; Richter 1948; Longwell 1951; Liscinsky 1972; K. J. Gutzwiller and K. R. Kinsley, unpublished data). Thus, the acreages of nonstocked forest areas and pastureland may serve as indices of the amount of habitat available for use by displaying males.

Studies of roosting habitat have not been conducted in Pennsylvania, but reports from other areas indicate that singing grounds and other openings with similar vegetative characteristics are used as nocturnal roosting sites (Krohn 1971; Dunford and Owen 1973; Wishart and Bider 1976; Nicholson et al. 1977). Thus, nonstocked forest areas and pastureland may also serve as indices of available roosting habitat.

Liscinsky (1972:59) found that woodcock in Pennsylvania frequently use coverts "composed of shrub, brush, or low tree-type vegetation" during their daily resting or loafing periods. Therefore, sapling–seedling stands may satisfy the habitat needs of woodcock for diurnal cover.

Old fields, brushy edges, shrub and small-tree thickets, and young second-growth timber are used by nesting woodcock in Pennsylvania (Yerger 1947; Liscinsky 1972; Coon 1977; K. R. Kinsley, unpublished data). The land-use categories that may best reflect these habitat conditions are nonstocked forest areas and sapling–seedling stands.

Specific information describing structural characteristics of brood habitat in Pennsylvania is not available. However, the general consistency among various descriptions of brood habitat in other areas suggests that certain habitat conditions are required by broods, regardless of geographic location. Reports by Mendall and Aldous (1943), Sheldon (1967), Wenstrom (1974), and Bourgeois (1977) indicate that broods use edges, open fields, young open forest, brushland, and areas occupied primarily by saplings and seedlings. Presumably, broods in Pennsylvania use similar types of habitat. Thus, acreages of nonstocked forest areas and sapling–seedling stands may also reflect the amount of potential brood habitat.

Habitat Trends and Information Voids

In a preceding section, we indicated a decline during the last decade of land-use categories potentially beneficial to woodcock, such as pastureland, sapling–seedling stands, and nonstocked forest areas. We also noted an increase in sawtimber and in urban and built-up areas, which generally are not suitable to woodcock. These trends are consistent with the apparent decline in Pennsylvania's breeding woodcock population during the same period.

We predict that the amount of pastureland in Pennsylvania will not change much in the coming years. If urban and built-up areas in Pennsylvania expand, as we have predicted, then areas of potential value to woodcock will be continually lost. Forest land classes are expected to decline during the next 10 to 20 years, with the exception of an increase in sapling–seedling stands. In general, these projections do not provide a very optimistic view of the future availability of woodcock habitat in Pennsylvania.

Clearly, the existing data are not detailed enough to enable us to make more definitive statements than we have made here. There are some voids apparent in the data. For example, we need information that will enable us to identify the habitats needed by both sexes and all age classes of woodcock throughout the year, not only in Pennsylvania, but throughout the woodcock's geographic range. We need to know which characteristics determine the quality of these various habitats. And, we need the ability to relate these habitat needs to land-use categories that are more refined than the broad categories discussed thus far.

Several pending improvements in the accuracy and coordination of land-use data are worth noting. The SCS is now implementing a nationwide inventory of land usage and allied site characteristics, as mandated by the Resources Conservation Act of 1977. Within Pennsylvania, a prototype survey, completed in 1977, involved 0.6% of each county's land area. This preliminary survey will be followed by a more detailed survey in 1982, which will involve a minimum of 4% of each county's area and include on-site evaluations of land use, soil conditions, vegetative cover, wetlands, and wildlife habitat. The national data base will be maintained at Iowa State University and updated every five years.

A compromise may also be established between SCS and FS land-use definitions through a new assignment accepted by the U.S. Geological Survey. A new project will place the responsibility for making national land-use classifications with the Survey; high-altitude photography will be used as the working medium for this data base. A standardized land-use classification system will also be developed as a coordinated effort among the various agencies having interests in this central project (Hirsch et al. 1979:355–356).

However, we will still need to know how this land-use information relates to the habitat needs of woodcock. And, we will still need to know which land-use categories provide the best habitat for the woodcock's activities throughout its annual cycle. The following section describes a consolidated research framework through which voids in the data base can be filled.

Framework for Future Research and Management

A primary goal of management is to maintain high-quality environments for woodcock. To achieve this goal, it is apparent that better information is needed to fill the voids in our knowledge of this species. Despite efforts to improve existing information, we still need better techniques to survey woodcock populations and to classify, evaluate, and inventory habitat suitable for woodcock. Finally, we must plan to obtain financial support for critical research and management activities. This support can only be obtained after the important research and management needs have been clearly defined

Specific recommendations concerning research and management for woodcock were first outlined by Liscinsky (1966) and later elaborated by Owen (1977). These recommendations have led to some significant research; however, no real attempt has been made to integrate these data so that major problems, research needs, and management goals can be clearly understood by resource managers.

We believe that a conceptual framework is needed to put the overall woodcock-management program into better focus. Such a framework would: (1) outline the basic components of the program and enable individual researchers to relate better to an overall strategy, and (2) serve as a guideline for integrating appropriate data bases from local areas to help solve regional problems. In short, such a framework would serve as a guide for an effective long-range woodcock-management program.

A research and management framework may be divided into the following three components: I, habitat classification and evaluation; II, inventory and trends; and III, decision making (Fig. 2). The first component consists of two phases, and the two remaining components consist of one phase each.

Phase 1 of component I consists of classifying all land into appropriate land-use categories and habitat types. This includes lands and habitats that are used, as well as those avoided by woodcock. The classification and inventory of all land would aid the management of not only woodcock, but also other species. In addition, a complete classification would enable managers to monitor land-use categories that are either bene-

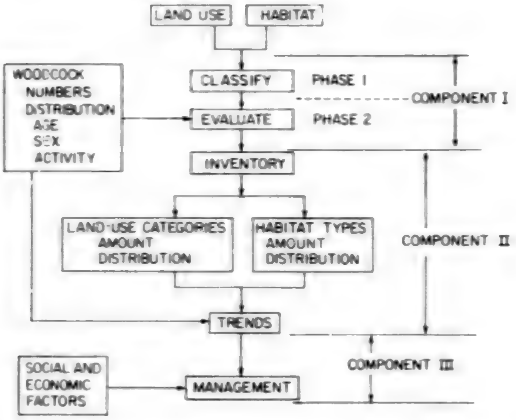

Fig. 2. Flow diagram of conceptual framework for future woodcock research and management.

ficial or detrimental to woodcock. The second phase, involving an integration of data concerning land use, habitat selection by woodcock, and woodcock numbers, distinguishes among land classes of differing value to woodcock. This step identifies land-use categories and habitat types that best satisfy the woodcock's habitat needs during its annual cycle. Such a step might involve: (1) the establishment of key study areas throughout the woodcock's range where biologists can monitor woodcock numbers and compare these numbers to habitat types on a long-term basis, and (2) a comparison of woodcock population data with land-use and habitat information at local and regional levels. Together, the first and second phases would provide information regarding the availability of potential woodcock habitat and the types of land and habitat preferred or avoided by woodcock.

Only recently have researchers undertaken studies to determine the quality of specific habitats (Dobell 1977; Gutzwiller 1980; T. J. Dwyer, personal communication), even though this type of work was a primary recommendation of Owen (1977). We submit that intensive studies of habitat selection by woodcock should continue to receive high priority in the overall research framework.

When the habitats suitable to woodcock have been identified, component II of the conceptual framework can be implemented. This component centers on the inventory of woodcock populations and the lands and habitats that support woodcock. Woodcock population surveys have been and continue to be coordinated by the U.S. Fish and Wildlife Service. Although State and Federal researchers have worked to develop better census techniques, room for improvement still exists (Godfrey 1975; Owen 1977). More accurate information regarding woodcock harvests and hunter success would also prove valuable in monitoring woodcock numbers.

Perhaps the most critical needs are to determine the amount and distribution of woodcock habitat and the changes in these items over time. To obtain such information, we believe it is necessary to:

- Continue support of the ongoing efforts by State, Federal, and private organizations to inventory land use and habitat on a regional and national scale.
- Expand the initial effort by T. J. Dwyer (unpublished data) to monitor changes in singing-ground habitats along survey routes.
- Inventory habitat on a regular basis at the local and regional levels so that trends can be identified and considered in management decisions.

To implement the activities outlined in components I and II, it will be necessary to obtain increased financial support from existing public and private sources (Sandfort 1977), and identify new sources of funding (Labisky et al. 1979) for the support of long-term studies on a regional scale.

Component III in the conceptual framework for woodcock research and management is essentially a decision-making process related to socioeconomic forces, changes in woodcock populations, and trends in woodcock habitat. As indicated earlier, changes in human populations and energy supply and demand are the primary factors affecting land use and wildlife habitats. If the current trend of increasing human population and energy consumption continues, it is axiomatic that pressures on land for uses other than wildlife habitat will intensify. As the amount of land suitable to woodcock dwindles, the importance of habitat management on remaining, undeveloped areas will increase. Thus, the need to inform landowners about habitat management (Coulter and Baird, this volume) that can be practiced on a local scale cannot be overemphasized. An effective extension and education program will play an important role in conveying such information to the public and gaining support for decisions arrived at through component III.

Summary and Conclusions

On the basis of singing-ground surveys coordinated by the U.S. Fish and Wildlife Service, we conclude that the breeding woodcock population in Pennsylvania has declined from 1967 to 1980. Pastureland, sapling–seedling stands, and nonstocked forest areas, potentially useful to woodcock, declined in Pennsylvania from the mid-1960's to the late 1970's, and sawtimber and urban and built-up areas, generally not suitable to woodcock, increased. These land-use trends are consistent with the apparent decline in the breeding woodcock population in the state.

During the next 10 to 20 years in Pennsylvania, we predict further increases in urban and built-up areas, little change in acreages of pastureland and cropland, and declines in all forest stand classes except sapling–seedling stands, which will increase. In general, the declining trend in the availability of potential woodcock habitat in Pennsylvania is expected to continue.

Existing data on land-use and habitat needs of woodcock are inadequate to make accurate projections of habitat availability or to suggest ways of offsetting habitat losses. We therefore present a general framework to help guide woodcock research and management on a rangewide basis. The information obtained through this framework should enable managers to propose ways of reversing declines in habitat quantity and in woodcock numbers.

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Response of Several Game Species, with Emphasis on Woodcock, to Extensive Habitat Manipulations[1]

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Abstract

In 1971, the Michigan Department of Natural Resources began a program of reclaiming the intolerant stage of forest succession to increase the white-tailed deer (*Odocoileus virginianus*) population. This program allowed Wildlife Research to devise a research project to evaluate the effects of large-scale habitat manipulation on animal populations associated with the intolerant stage and on attitudes of the user public. Six experimental areas, totaling 140 km², were clearcut, two each at 25, 50, and 75% of the area. Woodcock (*Philohela minor*) populations were monitored by singing-male counts, ruffed grouse (*Bonasa umbellus*) populations by spring-drumming male counts, and deer populations by spring deer-pellet surveys and summer track counts. Numbers of singing male woodcock increased in proportion to the percentage of area cut; grouse have not responded to the treatment as yet; and deer increased the most on areas cut at 50% and least on areas cut at 75%. A concurrent study of the user public found that hunters agreed with cutting; grouse and woodcock hunters also reported a high proportion of good and very good hunts.

The State of Michigan has 2.43 million ha (6 million acres) of public land, of which 1.42 million ha (3.5 million acres) are in state ownership. Most of this land is used for growing timber and for meeting the recreational needs of the general public. Through land management, several different ecological stages can exist simultaneously, and this makes it possible to determine the amounts of certain forms of recreation that will be available. Logically then, a guide for land management based on the timber resource and demands for recreation is needed.

In 1971 the Wildlife Division of the Michigan Department of Natural Resources (DNR) began a program of habitat management to increase the white-tailed deer population. The Forest Wildlife Research Unit of the DNR developed a research program to evaluate the intolerant stage of forest succession relative to the goal of increasing the deer population. Preliminary results on deer and vegetation production, costs, and

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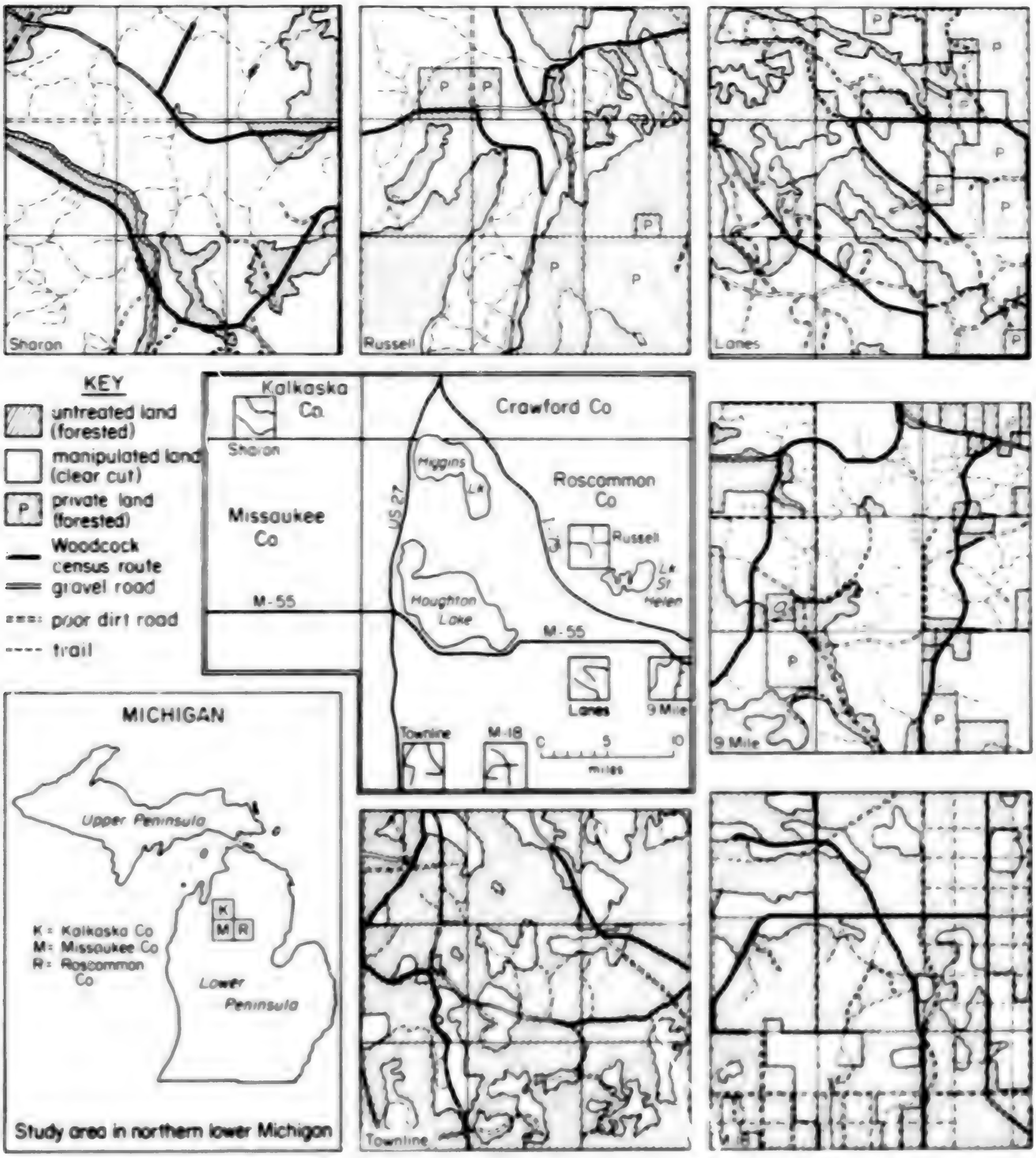

Fig. 1. Location of the six experimental areas in northern lower Michigan showing treated and untreated tracts.

human reactions to cutting were reported in Bennett et al. (1980). The present paper describes the response of woodcock, ruffed grouse, and deer to the intolerant stages of forest succession.

The Study Area

The study area was located in Roscommon and Kalkaska counties in northern lower Michigan (Fig. 1). Upland forest vegetation of the region is dominated by communities of second-growth aspen (*Populus* spp.), oak (*Quercus* spp.), and pine (*Pinus* spp.). The experimental areas were typical of public-ownership lands, with the usual history of pine logging at the turn of the century followed by wildfires, clearing, and grazing. Lowland swamps and drainage margins are characterized by stands of cedar (*Thuja occidentalis*), spruce (*Picea* spp.), and balsam (*Abies balsamea*) with alder (*Alnus* spp.) edges and pockets.

Topography of the areas grades from flat, to rolling, to hilly. Soils are generally sandy on outwash plains, changing to sandy loams on uplands and morainic slopes. Lowland soil includes poorly drained organic soils in bogs and swamps, with silty bottomlands along drainage-ways.

Average annual precipitation in the region is about 76 cm. Snow cover can be expected by mid-November and persists for about 100 days. Total annual snowfall varies from 200 cm in the Roscommon County area to more than 292 cm in Kalkaska County. Maximum snow depth ranges from 30 cm in the Roscommon County area to 45 cm on the Kalkaska County area. The mean annual temperature is approximately 7° C. The growing season varies from 80–120 days.

Methods

Design and Treatment

The studies were conducted on six separate 23.3-km^2 (9-mi^2) experimental areas. Treatment on the three pairs of areas consisted of clearing all standing trees from designated parts of the areas, which resulted in clearcuts totaling 25, 50, and 75% (Fig. 1). This range of treatment levels was necessary because: (1) the treatments had to be large enough to override activity on adjacent lands (especially on adjoining private land over which there was no experimental control), and (2) the difference between levels of treatment had to be large enough to enable measurement of the responses. Clearing on the experimental areas began in winter 1972–73, with completion dates of June 1973 for the 25%, June 1974 for the 50%, and June 1975 for the 75% areas.

The first priority method of treatment on the experimental areas was by commercial timber sales. Residual and nonmerchantable stands were leveled by handcutting, bulldozer with a tree cutter K-G blade, rolling chopper, or fire. Each method was applied to at least 15% of the total area treated on each experimental area.

First priority of vegetative types to be treated was mature aspen, followed by northern hardwoods (*Fagus* spp., *Betula* spp., *Acer* spp.), oak, jack pine (*Pinus banksiana*) mixtures, and then upland brush. All swamp conifers and most stands of upland conifers were left standing to provide winter cover.

Animal Population Monitoring

Woodcock

Two 6.4-km (4.0-mi) census routes were used on each experimental area to evaluate woodcock response (Fig. 1). Each route consisted of 10 listening stations at intervals of 0.64 km (0.4 mi). The total amount of clearing along the two routes combined was commensurate (± 5%, based on linear measurement at the road edge) with the prescribed treatment of that experimental area. Routes were nonoverlapping and located in the interior portion of the areas whenever possible. Shorter routes were necessary on one of the 50% areas (Russell) to attain the desired amount of clearing.

Censuses were conducted between 25 April and 15 May from 1975 to 1980. Three censuses of each experimental area were made in 1975–76 to estimate within-year variation; only one census of each route was made in 1977–80. Starting times and weather conditions for censusing followed guidelines established by the U.S. Fish and Wildlife Service, which are based on studies by Westall (1954), Blankenship (1957), Goudy (1960), and Duke (1966). Routes within experimental areas were censused simultaneously. The number of displaying woodcock identified in a 2-min period were recorded at each listening station. Counts for the two routes within an area were averaged for comparison with other areas. For the purpose of our analysis, a listening station was considered active for the year if at least one woodcock was recorded at the station.

To determine why woodcock used some clearings for singing grounds and not others, we recorded plant species and structural measurements for each listening station that occurred in a clearcut. The measurements included visual evaluation of the dominant species of regeneration (aspen, oak–maple, or other), the average height of regeneration (0.0–1.9, 2.0–3.9, or 4.0+ m), and the average density of regenerating vegetation (0–25, 26–50, 51–75, or 76–100% cover). In addition, a record was made of all major community types (aspen, conifer, oak, and mixed deciduous–conifer) bordering the clearing within 250 m of each listening station. Chi-square and discriminant function analyses were used to test the significance and relative importance of each of these factors.

Ruffed Grouse

Census routes and listening procedures for ruffed grouse followed those outlined by Newhouse (1975). Counts were made on all experimental areas during 1973–75 and in 1978 and 1980. A census route consisted of 20 listening stops at least 0.8 km apart; each route was driven twice on each of the experimental areas during May. The 2-h census period began 45 min before sunrise. The listening period at each stop was 4 min, during which the number and direction of all drummings were recorded.

Deer

Two field methods were employed to monitor changes in deer populations: spring pellet-group surveys (Eberhardt and Van Etten 1956) to estimate overwinter populations, and summer roadside track counts (Daniel and Frels 1971). Both surveys were begun in 1972 and continued through 1980.

Pellet surveys were conducted on the 25% clearcut areas in 1972, 1975, and 1978; on the 50% clearcut areas in 1973, 1976, and 1979; and on the 75% clearcut areas in 1974, 1977, and 1980. Each of the nine sections on an experimental area was sampled on the basis of random starting points. A total of 35 courses were selected, with four 81-m² (0.02-A) plots per course. The number of pellet groups per plot were counted and converted to an estimate of density using Ryel's (1971) formula.

Track counts were made during July and August on a 16-km route along poor dirt and gravel roads in each experimental area. On each route, three to five different track counts were conducted during the census period. Each route was dragged in the evening and the number of deer crossings counted the following morning.

Results and Discussion

Woodcock

Census results indicate that woodcock populations increased substantially on all six experimental areas between 1975 and 1980, totaling 290, 250, and 360% for the 25, 50, and 75% treatment levels, respectively (Fig. 2). Analysis of variance for treatment differences in each year (using a pooled estimate of within-year variation computed from replicate censuses in 1975–76) showed that the 50 and 75% treatment areas had significantly more ($P<0.05$) male woodcock than the 25% areas for all six years. Only since 1979, however, have all three treatment levels been significantly different ($P<0.05$) from each other. Also, the number of singing males has become proportional to level of treatment on the experimental areas since 1979.

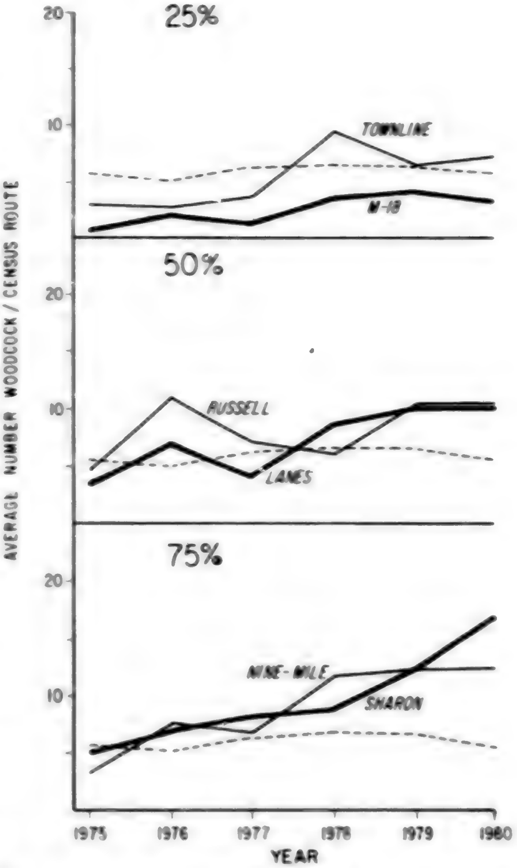

Fig. 2. Average number of singing male woodcock per census route for each experimental area, and regional census trends (dashed line) based on 31 woodcock census routes of the U.S. Fish and Wildlife Service in northern lower Michigan.

Experimental areas were compared to regional population averages for the same period. These comparisons show that all six experimental areas were below the regional average in 1975 and that the 50 and 75% experimental areas surpassed the regional levels in 1976 and remained higher (except for one unit) in 1977 (Fig. 2). In contrast, the 25% experimental areas generally remained at or below regional averages throughout the study. Because the regional population index re-

Table 1. *Number (percentage) of the listening stations in clearings used and not used by displaying woodcock in relation to the occurrence of various plant communities in and around the clearing.*

	Clearings			
	1976		1980	
Plant communities	Used	Not used	Used	Not used
Aspen community bordering clearing	33 (82)[a]	7 (18)	34 (85)[a]	6 (15)
Oak community bordering clearing	29 (64)	16 (36)	31 (69)	14 (31)
Pine community bordering clearing	41 (63)	24 (37)	45 (69)	20 (31)
Aspen dominant species in clearing	28 (66)	15 (34)	49 (83)[a]	10 (17)
Oak-Maple dominant species in clearing	14 (61)	9 (39)	9 (50)[b]	9 (50)
Total number of clearings	53 (63)	31 (37)	62 (74)	22 (26)

[a] Significantly greater use than randomly expected ($P < 0.05$).

[b] Significantly less use than randomly expected ($P < 0.05$).

mained relatively constant while treatment areas increased substantially, we concluded that spring population changes on the experimental areas were a result of the habitat alterations and not merely a reflection of regional population trends.

Comparisons of active and inactive listening stations to the occurrence of various plant communities revealed that clearings bordered by untreated aspen communities were used by singing male woodcock significantly more often in 1976 and 1980 (Table 1) than would randomly be expected ($P<0.05$). In addition, aspen-dominated clearings were used preferentially in 1980, whereas clearings dominated by oak and maple were apparently avoided. None of the other plant community or structural variables showed a significant relation to singing-ground use in either year.

Discriminant function analyses were then used to investigate the relative importance of plant species and structural variables in both years (Table 2). Significant results ($P<0.01$) were obtained in 1976 and 1980, and the functions were able to correctly classify 74 and 75% of the active and inactive listening stations, respectively. Although the discriminant function coefficients indicate that in 1976 the most important variable (35% explained variation) was the presence of bordering aspen communities, this variable ranked second to aspen regeneration in the clearings by 1980. The results of both habitat analyses support each other and suggest that the presence of aspen diurnal cover in proximity to a clearing may be more important than the overall structural composition within a clearing. Hale and Gregg (1976) found that woodcock would re-

Table 2. *Summary of discriminant function analyses for used and non-used listening stations by displaying male woodcock in relation to habitat variables in and around the clearings, including the discriminant function (D.F.) coefficients and its percent relative contribution to the overall function.*

	Clearing			
	1976		1980	
Habitat variable	D.F. coefficient	Relative contribution (%)	D.F. coefficient	Relative contribution (%)
Aspen community bordering clearing	1.22	34	-0.49	20
Oak community bordering clearing	-0.16	4	0.28	12
Pine community bordering clearing	-0.13	3	0.30	12
Aspen dominant in clearing	-0.65	18	0.84	35
Oak-Maple dominant in clearing	-0.72	20	0.03	1
Height of vegetation in clearing	0.53	4	-0.05	2
Density of vegetation in clearing	-0.23	6	0.45	18

spond to clearcutting only if it was done within 1.5 km of nesting or diurnal cover. Woodcock are known to be opportunistic in their use of openings for singing grounds (Mendall and Aldous 1943; Blankenship 1957), and Sheldon (1967) stated that the only consistent requirement for a singing ground is a "get away" aerial route.

Three of the experimental areas (Russell, Lanes, and Nine-Mile) experienced significant increases in the number of active singing grounds in the first two years after treatment, followed by a one- to two-year decline, and then further increases (Fig. 2). Similar patterns of increase and decline were also documented by Hale and Gregg (1976) for aspen clearcuts in Wisconsin and by Sepik et al. (1977) for alder cuttings in Maine. However, in both of these studies, the decline in use continued without further increases and was attributed to rapid regeneration of woody plants which reduced the suitability of the clearings for singing and roosting activities. We believe the initial response to our experimental areas may represent woodcock exploration of newly created (1976) singing-ground habitat, some of which were found to be undesirable and abandoned, resulting in the 1977 decline. One instance in particular involves a singing ground on the Nine-Mile area located more than 600 m from the nearest diurnal cover; it was used in 1976, abandoned in 1977, and not used again until 1979.

Over the six years of monitoring, the total number of active listening stations increased from 38 to 62, and the average number of birds per listening station increased from 1.0 to 1.9, indicating greater overall use of the experimental areas in terms of density and distribution of singing grounds. The increases were most pronounced on the 75% treatment areas. Increases in active listening stations on the 25% areas were less dramatic because the clearcuts were smaller, allowing woodcock to use the entire clearing immediately after cutting.

The immediate increases in singing-ground activity on the experimental areas were associated with the clearing of mature forests, while the long-term increases appeared to be more a result of subsequent aspen regeneration within the clearings. Woodcock require an interspersion of forest and field activities (Mendall and Aldous 1943; Blankenship 1957; Sheldon 1967). Immediately after cutting operations on the experimental areas, our observations indicated that interspersion requirements were met only along untreated forest edges. Within a year, however, aspen, cherry (*Prunus* spp.), and other early successional species responded to the favorable growing conditions. Locations originally dominated by mature oak, maple, and pine did not regenerate as rapidly and tended to remain as grassy openings much longer. As the regenerating aspen matured, creating a finer-grained interspersion of forest and field habitats, the total amount of habitat available to the birds increased. This conclusion is supported by the extended distribution of singing grounds and the first reports of woodcock nesting and raising broods within the regenerating aspen, starting in 1978.

Monitoring has not continued long enough to determine whether the experimental areas have reached optimal conditions for woodcock. Our present information suggests that the 25 and 50% areas may have peaked in 1978 and 1979 respectively (five years after treatment), while the 75% areas are still showing regular increases. Certainly, however, the maximum number of displaying woodcock that can be supported on any of these areas is a function of the original forest composition and of the amount and interspersion of forest regrowth within the clearcuts.

Ruffed Grouse

Ruffed grouse drumming activity varied between 0.2 to more than 2.5 drumming sites per listening stop (Fig. 3). Russell and M-18 values are conservative, since the presence of operating oil pumps in both areas in 1978 and 1980 interfered with audibility of the drumming. The drumming censuses conducted since 1973 do not appear to show any patterns in drumming-male use of the experimental areas that can be related to treatment levels. Moran et al. (1980) suggest that the drumming counts are similar to fall flush rates reported from cooperating hunters and postcard surveys conducted to estimate kill. They suggest that there was a positive relation between the number of drumming males and habitat diversity.

Among investigators there is a consensus that the shrub layer of vegetation is one of the most important determinants for drumming males (Palmer 1963; Boag and Sumanik 1969; Boag

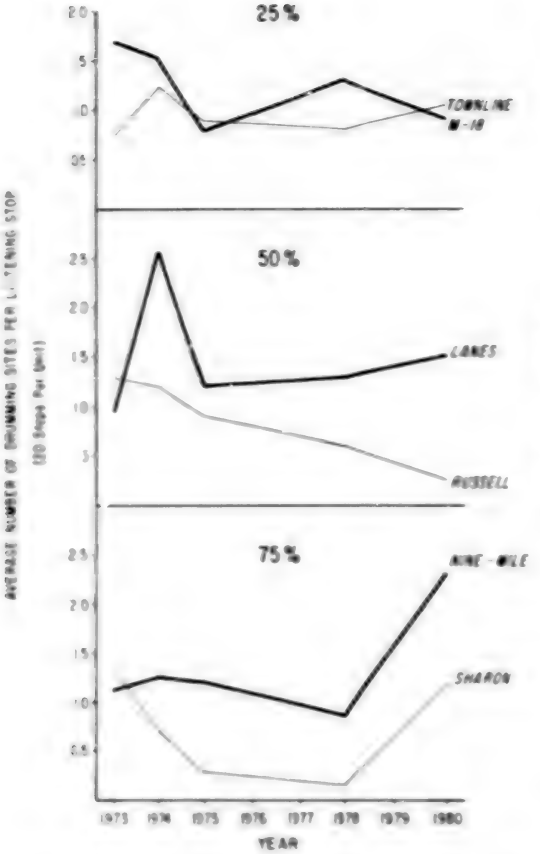

Fig. 3. Average number of ruffed grouse drumming sites per listening stop for each experimental area. The 1973-75 data are from Newhouse (1975), and the 1978 and 1980 data are from Moran *et al.* (1980).

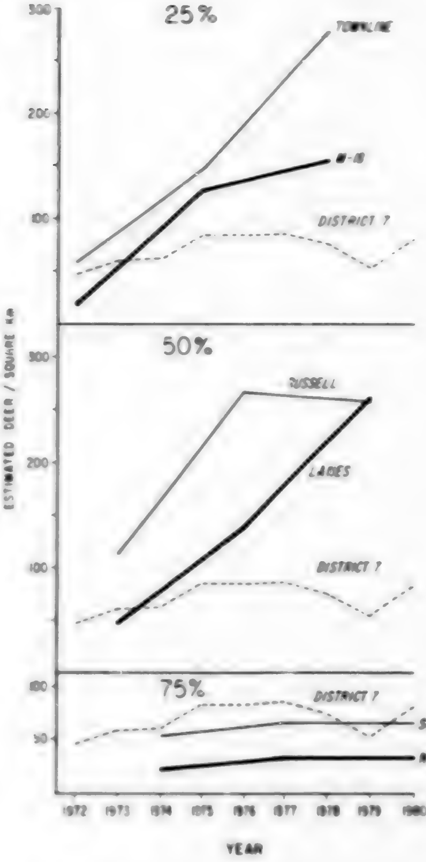

Fig. 4. Trends in overwinter deer populations on experimental areas and surrounding locale (dashed line) according to spring pellet group surveys, northern lower Michigan.

1976; Stoll et al. 1979). Stoll et al. (1979) found that cover types in a 16-ha area around traditional (perennial) drumming sites included three times as much brushland and heavily cut woodland. During prelaying and laying periods, female grouse prefer lowland alder and mixed hardwood habitats and avoid open fields and marshes (Maxson 1978). Large recent clearcuts, therefore, would not be expected to encourage use by drumming males and nesting females and, predictably, no pattern of response in the experimental areas is yet apparent. Vegetative growth on the experimental areas should soon begin to meet the habitat needs of grouse, and their response may become pronounced in the future.

Deer

Overwinter densities of deer, estimated by spring pellet-group surveys in 1972, were about 25 to 60 deer per km² on the 25% experimental areas and for the Michigan DNR district in which the study was located (Fig. 4). Densities of deer showed a steady increase of 20 to 35/km² per year on the experimental areas through 1978, while densities in the DNR district remained steady between 50 to 75/km². A similar pattern of increase was recorded for the 50% experimental areas between 1973 and 1979, with deer densities approaching 250 to 275/km². Densities remained between 20 and 60/km² on the 75% experimental areas between 1974 and 1980 and were somewhat less than densities recorded for the DNR district.

Additional field observations and other studies dealing with deer behavior and wintering deer food-shelter relations (Ozoga and Gysel 1972) also suggest that the 75% clearcut area will not

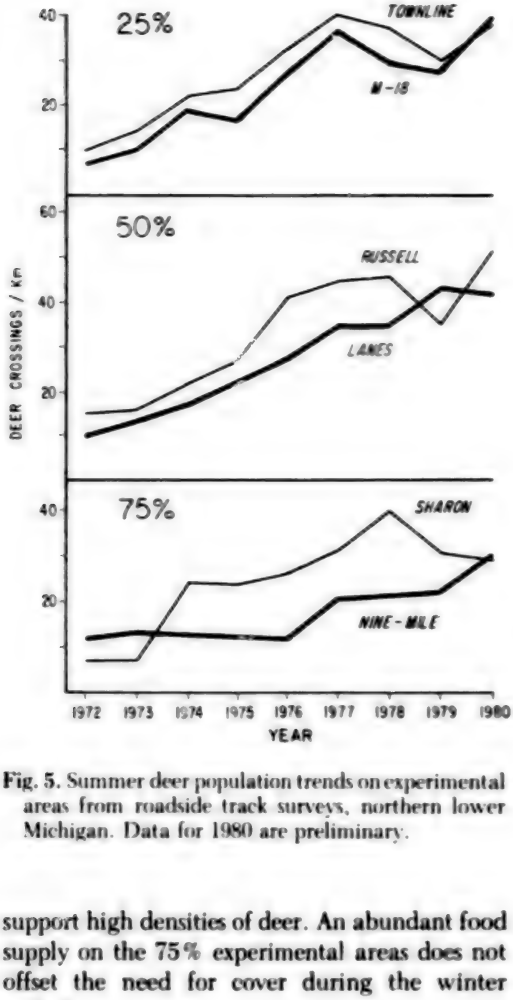

Fig. 5. Summer deer population trends on experimental areas from roadside track surveys, northern lower Michigan. Data for 1980 are preliminary.

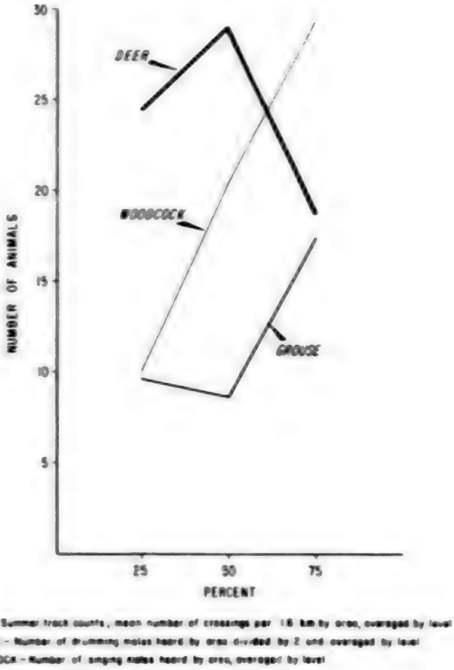

Fig. 6. Comparison of deer, grouse and woodcock populations, by treatment level for 1980 on experimental areas, northern lower Michigan.

support high densities of deer. An abundant food supply on the 75% experimental areas does not offset the need for cover during the winter period.

The number of deer crossings per kilometer of road started at approximately 5 to 15 in 1972 and increased to nearly 50/km on the 25 and 50% experimental areas by 1980 (Fig. 5). Although the number of crossings on the 75% experimental areas increased from 1972 to 1980, the number of crossings in 1980 were less than those observed in the 25 and 50% experimental areas. Numbers of deer at the DNR district level, based on pellet counts, remained constant during the time when we were recording increased summer use on the experimental units. This finding is consistent with the positive response to clearcut areas during July and August shown by Nelson (1979) and Stormer and Bauer (1980). They found that the response was due to extensive browsing of aspen leaves.

Conclusion

Three animal species classed as inhabitants of the young-aged early successional forest responded differently to large-scale experimental habitat manipulation. Greatest woodcock response was to the 75% experimental areas (Fig. 6). Ruffed grouse exhibited no response. Deer responded most on the 50% clearcut with a much suppressed response on the 75% areas—even below that on the 25% areas. These conclusions could change as the early successional forest continues to grow since the 75% areas are only six growing seasons old. It appears that these three species have a different hierarchy of limiting factors. If that is indeed true, the concept of key value becomes the management philosophy (Bennett et al. 1980).

As Sousa (1980) stated: "Most importantly, the processes of recolonization and species replacement following a disturbance which opens space are better explained by the life history characteristics of individual species than by any emergent properties (Salt 1979) of the whole community."

Deer hunters mostly agreed with the cuttings; woodcock and grouse hunters predominately agreed with cuttings and had high enjoyment ratings of the hunt (Langenau et al. 1979). Clearcutting in this area of the state elicited a large negative response neither from users nor from area residents (Langenau et al. 1977).

We recommend management aimed at a target species with sufficient advertising and planning to negate any possible adverse public reaction.

Acknowledgments

We wish to thank the many people in the Michigan DNR who have been involved in this project including the Houghton Lake Wildlife Research Station staff (in particular, Richard Moran), the foresters and forest fire personnel of the Forest Management Division, and the management personnel of the Wildlife Division.

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Woodcock Response to Habitat Management in Maine

by
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Abstract

A study was initiated in 1975 at the Moosehorn National Wildlife Refuge to develop habitat management techniques for woodcock (*Philohela minor*) that could be used by small landowners as well as in commercial forestry operations. Use of selected diurnal covers by adult female and juvenile woodcock increased after strips were clearcut through these covers. Woodcock use of clearcut strips for feeding was equivalent to that in adjacent uncut areas after only 6 years of growth. Small clearings created by firewood cutters in a 1,200-ha hardwood stand increased singing male activity, but commercial forest operations were necessary to increase singing-male use in relation to the rest of the refuge. The age structure of courting males on new clearings favored second-year males (65%), but older males (55%) were more common on established singing grounds. Spring burning of commercial-quality blueberry fields increased roosting activity during the summer of the burn. Roosting woodcock also preferred clearcuts adjacent to active summer fields in which the slash had not been treated. Management recommendations are also given.

Woodcock numbers in the Northeast have been gradually declining over the past decade (Artmann 1977). One of the most pressing problems is a deterioration in the quality and quantity of habitat as a result of urbanization, intensive forest management practices, fire control, and a decline in farm abandonment. Management of existing habitat has therefore become increasingly important.

Mendall and Aldous (1943) first demonstrated the value of habitat management for woodcock at the Moosehorn National Wildlife Refuge in Maine. They found that artificial clearings were used by courting males, and they recommended clearcutting, thinning, and burning as possible management techniques. In subsequent studies at Moosehorn, Rearden (1950) found that woodcock showed a preference for managed covers. Liscinsky's (1972) Pennsylvania study also demonstrated a variety of habitat improvement techniques, including clearcutting, selective cutting, and herbicide application. In Wisconsin, Hale and Gregg (1976) found that feeding and roosting woodcock made heavy use of clearcuts in aspen (*Populus* spp.).

In 1975 a study was initiated at the Moosehorn National Wildlife Refuge to develop woodcock management techniques that could be used by small landowners and in commercial forestry operations. Special efforts were made to record changes in woodcock use of covers that were altered by management. Initial findings (Sepik et al. 1977) showed an increase in woodcock use of diurnal covers where 20% of the vegetation was clearcut and an increase in the use of small clearcuts in a large contiguous hardwood stand by singing males. We present other aspects of the study in this paper and make further management recommendations.

Study Area and Methods

This study was conducted at the Baring Unit of the Moosehorn National Wildlife Refuge near Calais, Maine. When the refuge was established in 1937, the area was predominantly abandoned farmland and recently logged and burned forest. Today the area is 90% forested, with mixed stands of spruce (*Picea* spp.), balsam fir (*Abies balsamea*), and white pine (*Pinus strobus*). Predominant hardwoods include birch (*Betula* spp.), red maple (*Acer rubrum*), and aspen (*Populus* spp.). Alder (*Alnus rugosa*) is common on moist sites but is rapidly being replaced by later successional species. Most wooded areas have passed their prime for woodcock, thereby providing an excellent opportunity to test various management techniques.

Diurnal Cover Management

Rejuvenation of alder covers was attempted by clearcutting about 20% of selected covers in strips 10 to 20 m wide. These cleared strips were separated by uncut blocks 40 to 80 m wide. Slash was either piled and burned or chipped. Three alder covers have been monitored intensively since they were cut. Modified shorebird traps (Liscinsky and Bailey 1955) were used to measure woodcock use of the clearcut strips and uncut portions of covers, as well as six unmanaged covers.

Singing Ground Management

In 1974 a firewood-cutting program was initiated in a 1,200-ha hardwood stand. Local residents were assigned 30- × 30-m, or 1.3-ha, blocks to clearcut. In 1978 commercial clearcuts were started; these cuts were either 20 m wide and up to 400 m long, separated by 80- to 100-m uncut blocks, or 2-ha block cuts. Adjacent blocks or strips will be cut at 10-year intervals, resulting in a 40- to 50-year rotation.

Singing-male surveys were conducted on this area to document woodcock use before and after cutting. Our survey differed from the federal survey (Clark 1970) in that stops were only 0.5 km apart and the routes traversed the entire study area, so that all courting birds on the study area could be located. Throughout the course of this study, singing males were also captured on both newly created and traditional singing grounds using mist nets (Sheldon 1967).

Nocturnal Cover Management

Commercial Blueberry Management

Moosehorn National Wildlife Refuge contains several blueberry fields that serve as active summer roosting areas for woodcock. Four of these fields were placed in commercial blueberry management. Two of the fields, 1 and 10 (each 2 ha), were separated by a gravel road and 50 m of second-growth hardwoods. Field 1 was burned in April 1977 and Field 10 the following spring. Neither field had been burned for at least 5 years, but both had been mowed occasionally. A third blueberry field, 36 (also 2 ha), had been maintained by hand cutting invading woody vegetation; this field was burned in April 1977, but about 25% was left unburned to serve as a control. Blueberry Field 7 (3 ha) contained 1.5 m tall hardwood growth before it was mowed in August 1977; this field was burned in April 1978.

Woodcock use of the fields was monitored before and after burning using mist nets (Sheldon 1967). Fields were netted about once a week from 1 June to the end of August, but only data from the peak period of summer field use (12 June to 20 July) were used to analyze woodcock abundance.

The response of vegetation to fire was also measured during the peak of woodcock use. The number of stems by species and percent cover were recorded the summer before and after burning.

Enlarged Temporary Summer Fields

In the fall of 1978, Blueberry Fields 1, 10, and 39 were enlarged by 1.7, 0.4, and 1.0 ha, respectively. All merchantable wood was removed from these fields, and the remaining slash on 20 systematically distributed 0.25-m^2 plots in each field was oven dried and weighed. In June 1979 the enlarged portion of Field 1 was broadcast burned, and the amount of slash remaining was measured.

In the newly cut areas and adjacent fields, woodcock use was monitored throughout the summer by nightlighting (Rieffenberger and Kletzly 1967). The locations of initial flushes and captures were recorded.

Table 1. *Capture rates of adult and juvenile woodcock in diurnal cover 5 (DC 5) and unmanaged covers (UC) from 1974 through 1979 and the number of singing males using the clearcut strips, Moosehorn National Wildlife Refuge.*

		Capture rate[a]					
		Adult males		Adult females		Juveniles	
Year	No. of singing males in DC 5	DC 5	UC	DC 5	UC	DC 5	UC
1974	2	0.24	0.12	0.44[b]	0.15	2.44[b]	1.37
1975	3	0.84[b]	0.13	0.49[b]	0.23	2.45[b]	1.75
1976	2	0.11	0.04	0.26[b]	0.04	1.53[b]	0.75
1977	1	0.17	0.07	0.29[b]	0.13	1.17	0.91
1978	1	0.14	0.07	0.28	0.14	0.93	1.20
1979	1	0.03	0.07	0.11	0.08	0.37	0.39

[a] Capture rate = number of captures per 100 cell nights.

[b] Chi-square analysis indicated different capture rates for woodcock caught in diurnal cover 5 and unmanaged covers (df = 1, $P < 0.05$).

Response to Management

Diurnal Cover Management

Sepik et al. (1977) found increased use of diurnal covers after strips had been clearcut through the covers. They postulated that the clearings attracted courting males and this, in turn, attracted females. The females probably nested and raised their broods near the cover; thus the young gained an affinity for the area and remained there through the summer. To further test this hypothesis, from 1974 through 1980 we monitored not only the capture rates of juvenile and adult woodcock throughout the summer, but also spring singing-male use of unmanaged covers and of a cover that had been strip clearcut in 1973 (Diurnal Cover 5).

If overall woodcock abundance in a cover is a function of the presence of courting males, it should be reflected in the use of the cover by adult females and juveniles, and this was indeed the case in Diurnal Cover 5 (Table 1). As long as use by singing males remained high, the summer capture rates of adult females and juveniles were greater than those in unmanaged covers (X^2, df = 1, $P<0.05$). However, as the clearcut strips began to grow back and singing-male activity decreased, adult female and juvenile capture rates decreased, approaching those for unmanaged areas. Adult male capture rates exceeded those in unmanaged areas during 1975 (X^2, df = 1, $P < 0.05$), the peak of courting male activity in the strips. Apparently, male affinity for covers near their courtship area is not as strong as that exhibited by females and juveniles. However, during periods when competition between males is great, they may stay close to their courting area and thus gain an affinity for the area. Subdominant male activity may also be greater during such times.

Table 2. *Woodcock capture rates in the strips clearcut in 1973 and in the uncut portions of diurnal cover 5, Moosehorn National Wildlife Refuge.*

	Capture rate[a]		
Year	Clearcut portion of cover	Uncut portion of cover	Difference
1976	0.39[b]	2.47	2.08
1977	0.56[b]	1.96	1.40
1978	0.48[b]	1.50	1.02
1979	0.56	0.46	-0.10
1980	0.68	0.58	-0.10

[a] Capture rate = number of captures per 100 cell nights.

[b] Chi-square analysis indicated different capture rates for woodcock captured in the clearcut strips and uncut portions of the cover (df = 1, $P < 0.05$).

While capture rates in Diurnal Cover 5 as a whole were decreasing, capture rates in portions of the covers that were clearcut in 1973 were approaching those in uncut sections of the cover (Table 2). From 1976 through 1978, few woodcock were captured in the strips, but in 1979 capture rates in uncut and clearcut areas were not

Fig. 1. Small clearings (30 × 30m) were created in a 1,200 ha hardwood stand at Moosehorn National Wildlife Refuge to provide singing grounds.

different (X^2, df = 1, $P < 0.05$). During the sixth growing season, the vegetation had reached a stage at which woodcock usage was about the same as in the adjacent older vegetation. Liscinsky (1972) stated that alder covers between 10 and 20 years old are most attractive to woodcock; therefore, woodcock use of the surrounding cover that is more than 20 years old should decrease while use of the strips should continue to increase.

Singing Ground Management

Although small clearings (30 × 30 m) created between 1975 and 1978 by firewood cutters (Fig. 1) in a 1,200-ha hardwood stand increased singing-male activity over that in the area before cutting (Table 3), there was little change in use relative to the rest of the refuge. In 1978, commercial forest operations were initiated in addition to the recreational firewood cutting. By the spring of 1979, the number of clearings had more than doubled, nearly all courting males were using artificial clearings, and singing males in the hardwood stand had increased to 18% of the refuge total. By 1980 there were 45 clearings 3 years old or less. The number of courting males was at a 7-year high, and 24% of the courting males on the refuge were in this hardwood stand. During this same period, the number of singing males had decreased throughout Maine (John Tautin, personal communication).

Since 1976 there has been a surplus of artificial clearings. However, until 1978 the surplus had been small and the clearings were not very large. With the advent of commercial harvesting, the clearings became more numerous and larger (Fig. 2). Many different age classes, shrub types,

Table 3. *Data on courting male woodcock use of clearcuts in a 1,200-ha hardwood stand at Moosehorn National Wildlife Refuge.*

		Courting male woodcock				
			In hardwood stand		Using clearcuts in hardwood stand	
Year	No. of clearcuts[a] in hardwood stand	In entire refuge (no.)	No.	%	No.	%
1974	0		9		0	(0)
1975	4		15		3	(20)
1976	11	72	12	(17)	6	(50)
1977	18	69	8	(12)	5	(63)
1978	21	64	10	(16)	3	(30)
1979	30	67	12	(18)	10	(83)
1980	45	66	16	(24)	14	(88)

[a] Only clearcuts less than 3 years old are considered as suitable courting areas.

and moisture gradients were crossed by the commercial cuts, resulting in an increase of the probability that a given clearing would provide the correct physiographic and vegetative parameters to attract courting males.

From 1976 through 1979, 179 courting males were captured throughout the refuge. The age structure of all males caught on clearings that were less than 1 year old was independent of the age structure on traditional singing grounds and older clearings (X^2, df = 1, $P < 0.05$). Second-year (SY) males were predominant on the new clearings and after-second-year (ASY) males on the other areas (Table 4). The age structure of the subdominant male population is probably similar to that of males on the new clearings. In fact, there was no difference between the age structure of subdominant males captured in sing-

Fig. 2. Commercial forest harvesting at Moosehorn National Wildlife Refuge provided numerous clearings which crossed a variety of age classes, shrub types, and moisture gradients.

Table 4. *Age distribution of courting males on established singing grounds and newly created singing grounds (1976–79), Moosehorn National Wildlife Refuge.*

	No. of courting males captured					
	On established singing grounds		In clearings less than 1 year old		No. of subdominant males captured	
Age[a]	No.	%	No.	%	No.	%
ASY	82	(55)	11	(35)	2	(15)
SY	66	(45)	20	(65)	11	(85)

[a] ASY = after second year; SY = second year.

ing grounds and that of dominant males caught in first-year cuts (X^2, df = 1, $P < 0.10$). If the clearings had not been made available, these dominant birds would probably have been nonbreeders. If courting males had simply shifted their singing grounds from an established (but marginal) area to a new, more attractive clearing, then the age structure of males on the two different areas would have been similar.

Fourteen active singing grounds were burned during the peak of courtship activities. Despite the great change in the character of the area caused by the fire, courting males continued to use the area without exception. This persistence suggests that the exact nature of the courtship area may not be as important as other surrounding characteristics. Whitcomb (1974) suggested that the quality of the brood habitat surrounding a clearing may influence the use of that area.

Nocturnal Cover Management

Commercial Blueberry Management

Summer roosting activities of woodcock increased in all fields the summer of the burn (Table 5). Woodcock use in 1977 was greater in Field 1 than in nearby Field 10, which had not been burned. Field 10 was burned in 1978 and, as a result, woodcock activity there surpassed that of Field 1 (Wilcoxin test, $P < 0.05$). Woodcock use of Field 36 increased in the year of the burn ($\mu = 0.42$ woodcock captures per net), but decreased the summer after the burn ($\mu = 0.12$ woodcock captures per net; t-test, df = 7, $P < 0.05$). A nearby unburned field showed no change in use during the same two years. Use of Blueberry Field 7 was greater in 1978, the year of the burn, than in 1977 (Wilcoxin test, $P < 0.05$).

Woodcock preferences probably changed because of the effects of the fire on vegetation. In the absence of fire, blueberry plants become bushy, with an individual plant covering a relatively large area. A spring or fall fire will prune the blueberry plant to the ground. The first year's growth is predominantly vertical, with little lateral branching and, as a result, the field is more open even though the fire also stimulates additional blueberry sprouting. The amount of bare ground varied from 3.7 to 8.4% the summer before burning. Between 21 and 29% of the fields were bare ground the summer of the burn, but in the following year the amount of bare ground decreased to its preburn level. The amount of area covered by blueberry plants was at its minimum the year of the burn.

Sweet fern (*Myrica asplenifolia*) was common in Field 36. One year after burning, sweet fern

Table 5. *Capture rate of woodcock by mist netting on two blueberry fields which were subject to spring burning on alternate years, Moosehorn National Wildlife Refuge.*

Date	Number of woodcock captures per net	
1977	*Burned/field 1*	*Control/field 10*
12–14 June	0.18	0.12
23–28 June	0.32	0.06
4–6 July	0.26	0.06
10–14 July	0.48	0.12
17–19 July	0.13	0.12
1978	*Burned/field 10*	*Control/field 1*
12–14 June	0.06	0.13
20 June	0.50	0.32
23–28 June	0.44	0.36
4–6 July	0.38	0.05
10–14 July	0.88	0.59
17–19 July	0.18	0.05

Table 6. *Number of woodcock observations on blueberry fields and adjacent clearcut areas in 1979, Moosehorn National Wildlife Refuge.*

	Number of observations/ha		
	Field 1	Field 10	Field 39
Established blueberry field	17.7	15.7[b]	3.4[b]
Adjacent clearing	10.8[a]	45.5[b]	16.2[b]

[a] Broadcast burned June 1979.

[b] Chi-square analysis indicated different capture rates in established blueberry fields and adjacent clearings.

covered 34% (31 stems/m^2) of the burned portion of the field, compared with only 11% in the unburned area (6.5 stems/m^2). When sweet fern becomes this abundant, woodcock use of a field is minimal. Continued burning would probably further stimulate sweet fern growth and make the field virtually unusable by woodcock the year after the fire.

Enlarged Temporary Summer Fields

Roosting woodcock preferred clearings cut adjacent to summer fields in which the slash had not been broadcast burned (Blueberry Fields 10 and 39). In established blueberry fields and in the clearing that was broadcast burned, usage was lower (Table 6; X^2, $P < 0.05$) than in areas where slash had not been burned. Slash loads on Fields 10 and 39 were 26.8 and 18.3 t/ha, respectively. The slash load in Field 1 was 23.3 t/ha before burning, but only 8.3 t/ha after the fire. Throughout the clearcut areas there were numerous scattered slash-free pockets where the woodcock roosted. Such areas probably provided more security than the open blueberry fields and the burned slash areas.

Conclusions and Recommendations

The initial increase in woodcock abundance after strip clearcutting through diurnal covers demonstrates both the potential and the need for continued habitat management of such areas. A 20- to 25-year rotation, as suggested by Liscinsky (1972) and Sepik et al. (1977), would maintain a cover at its optimum. Strips clearcut every 4 or 5 years should provide singing grounds, most of the cover should remain at its peak potential for woodcock use, and a drop in use like that seen in Diurnal Cover 5 would probably not occur. To obtain the rapid alder growth exhibited in Diurnal Cover 5, cutting during the dormant season would be necessary, and the cover must be located on good soils.

Apparently, some subtle difference exists between forest openings. Some clearings are never used by courting males, while others are used year after year. Therefore, numerous clearings are necessary to realize the full courting-male potential of an area. Short rotation times, with the cutting operations spread evenly over the rotation period, would be desirable and should provide an ample supply of singing grounds. However, even if these conditions cannot be met, the singing grounds should be maintained. Sporadic cutting, long rotations, or small-scale harvesting would not provide enough usable clearings each year. In most instances, sprout growth would render a clearcut unsuitable for use as a singing ground after only 3 or 4 years.

Among the preferred summer roosting areas for woodcock in the Northeast are blueberry fields. In Washington County, Maine, more than 4,400 ha of commercial blueberry fields are burned each year in the spring or fall to prune and prevent diseases (Amr Ismail, personal communication). Most fields are burned every other year and produce a crop the second year. Because a given field yields a cash crop only once every 2 years, most growers burn only half their acreage each year. In the present study, we found that blueberry fields which had recently been burned were favored by woodcock over nearby unburned areas. Commercial blueberry management dictates burning every second year. This practice, however, depletes the fuel supply, and commercial growers must either use specially designed propane or fuel-oil burners, or spread hay over the field to serve as a fuel source. This procedure is very labor intensive and expensive and would not be feasible if a field were to be maintained only for woodcock. A more appropriate strategy would be a burning rotation of 3 or 4 years, during which time enough fuel should have accumulated to make broadcast burning of the fields relatively cost effective.

Roosting woodcock showed a preference for clearcut areas with no slash treatment over the adjacent blueberry fields. Slash removal is therefore probably not necessary if an area is being cleared to create a summer roosting area. However, if the slash load is heavy, directional felling may be necessary to provide the scattered openings in the slash that are preferred by the birds.

Acknowledgments

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Breeding Woodcock Use of Manipulated Forest–Field Complexes in the Aspen Community Type[1]

by

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Abstract

We examined 23 aspen (*Populus tremuloides*) community habitat complexes in northern Michigan to determine usage by breeding woodcock (*Philohela minor*) relative to forest–field interspersion and food availability. We located 32 solitary birds and 31 broods during 78 h of daylight searching during the two years. Singing-male woodcock used 17 and 20 of the habitat complexes in 1978 and 1979, respectively. Three of the habitat complexes were not used at all during the study. Within habitat complexes, the between-year use by singing males and by solitary birds was much more consistent than use by broods. In 1979, a significant correlation existed between the number of broods using the habitat complexes and the number of singing-male woodcock. The most consistently significant relation existed between broods and earthworm abundance. The number of discrete openings and the abundance of earthworms were weakly correlated with the number of displaying males. Management considerations are discussed.

Researchers have long recognized that woodcock habitat includes a forest and a field component during both breeding and nonbreeding seasons (Pettingill 1936; Mendall and Aldous 1943; Blankenship 1957). In recent years considerable information has accumulated concerning the preferred structural elements of singing grounds (Maxfield 1961; Liscinsky 1972; Wishart and Bider 1976) and diurnal cover (Bourgeois 1977; Dyer and Hamilton 1977; Kroll and Whiting 1977; Rabe 1977). To apply this information effectively, we also need to understand how bird use relates to spatial associations of these habitat components. The objective of the present study was to investigate breeding woodcock response to variations in the interspersion of singing-ground and diurnal habitats.

Methods

The Habitat Complex

Our study was done within relatively homogeneous aspen plant communities of the Houghton Lake State Forest in the northern lower peninsula of Michigan. The sapling-size age class of aspen was selected because it is a preferred diurnal cover in that region (Blankenship 1957; Rabe 1977). A habitat complex was defined as the total area of a clearing, or cluster of clearings, plus a 50-m strip of surrounding aspen habitat (Fig. 1). Diurnal cover was limited to this amount based on results of Bougeois (1977) and Rabe (1977), who found that more than 90% of all diurnal contacts with woodcock (including nests, broods, and males) were within 50 m of a clearing.

We selected 23 habitat complexes for the present study. Areas were rejected if any other clearings were within 150 m of a defined complex. All clearings used in this study were mechanically created by using a rolling chopper to

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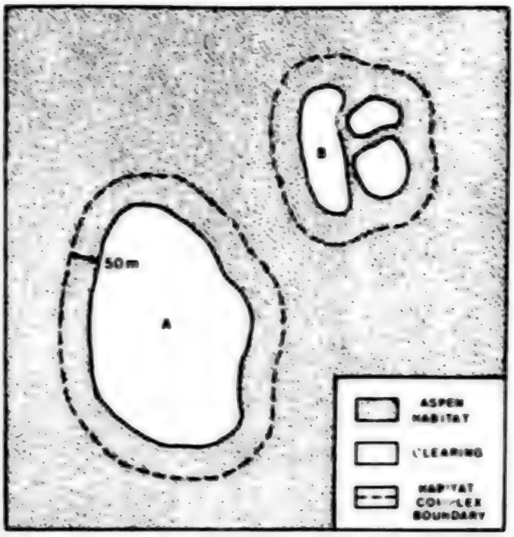

Fig. 1. Diagramatic representation of forest-field complexes with one (A) and three (B) discrete openings (see text for definition). The dashed line indicates the area of diurnal habitat included in each complex.

Table 1. *Mean and range of variables measured for each of the 23 habitat complexes to be evaluated relative to woodcock usage.*

Variable	Mean	Range
Area of aspen habitat (ha)	5.7	0.9–14.0
Area of clearing (ha)	2.5	0.1–10.9
Number of discrete openings	2.3	1 – 5
Shape of clearing[a]	2.2	1.1– 3.4

[a]Based on a formula for shoreline development by Wetzel (1975).

remove trees and destroy root systems. Five of the clearings were created in March 1978 and had only sparse plant cover during the study. Of the remaining clearings, 12 were created 3–4 years before the present study and planted to rye grass as part of a deer management program, and 6 were 8–10 years old and dominated by natural grasses and scattered shrubs, primarily sweet fern (*Comptonia peregrina*).

Variables measured for each habitat complex included size, shape, and number of clearings, and the amount of aspen (Table 1). Shape (S) was calculated as a ratio between the length of the perimeter of a clearing (L) and the circumference of a circle of equal area (A) and is based on a shoreline development formula presented by Wetzel (1975): $S = L/2\sqrt{\pi A}$. Discrete openings were defined as clearings larger than 0.1 ha that were individually isolated by a barrier of aspen trees (Fig. 1). Area and perimeter measurements were taken from aerial photographs using a computer digitizer.

Measurement of Soil and Earthworm Abundance

Food availability is an important component of habitat not easily controlled in experimental field studies. Therefore, earthworm abundance and soil moisture were monitored for possible influence on woodcock use of the habitat complexes. Since most feeding activity occurs in the diurnal habitat (Miller 1957; Dyer 1976), nine samples were collected at random locations in the aspen portion of each complex during May of both years. Earthworm abundance was measured in 0.25-m² plots using a formalin extraction technique (Reynolds et al. 1977). Soil moisture determination was made at the same site by a gravimetric method (percent moisture by weight). Soil moisture and earthworm abundance values were averaged for the analyses of each habitat complex.

Woodcock Use

Measurements of woodcock use included an evening census of singing males and diurnal searches of the surrounding aspen habitat with a pointing dog to locate broods and solitary birds. Singing-ground counts were done twice each year between 25 April and 15 May. Starting time and weather conditions for censusing followed guidelines established by the U.S. Fish and Wildlife Service which are based on studies by Westfall (1954), Blankenship (1957), Goudy (1960), and Duke (19[illegible]). The average of the two censuses was used in comparisons with other bird uses and habitat variables.

Three diurnal searches of the habitat complexes were made each year during the major hatching period, 1 May to 7 June. Searching was discontinued during rainy periods or when ambient temperatures exceeded 27° C, conditions that would impair a dog's ability to locate woodcock. An attempt was made to standardize searching effort among habitat complexes. Total contacts with broods and solitary birds for the

Table 2. *Maximum number of active singing grounds based on two censuses and total number to solitary birds and broods found during 39 h of searching each year (The value in parentheses is the percentage of the 23 habitat complexes used by woodcock.)*

Woodcock use	1978	1979
Singing males	26 (74)	35 (87)
Solitary birds	18 (39)	14 (35)
Broods	10 (26)	21 (43)

three searches were used in comparisons with other variables. When possible, all members of broods were banded to avoid recounts.

Results

Woodcock Use of Habitat Complexes

Observed numbers of singing male woodcock and of broods increased between 1978 and 1979, whereas contacts with solitary birds declined slightly (Table 2). Similar trends were also documented for the percentage of habitat complexes used by woodcock for these activities. The greatest change between years occurred in brood usage, where equivalent searching effort resulted in almost twice as many brood contacts in 1979.

Correlations between singing-male, solitary-bird, and brood use of the habitat complexes for 1978 and 1979 produced four statistically significant associations (Table 3). For the two years, the number of singing males and solitary birds were correlated ($r = 0.48$ and 0.44, respectively), and in 1979 the number of singing males was correlated with the number of broods using the habitat complexes ($r = 0.54$). Brood use in the two years was not significantly correlated ($r = 0.20$). A fourth significant correlation between singing males in 1978 and solitary birds in 1979 has little biological value.

Woodcock-Habitat Relations

Soil moisture and earthworm abundance increased slightly from 1978 to 1979 (Table 4). Although yearly averages of earthworm numbers did not change, numbers within some individual habitat complexes fluctuated.

Correlations between woodcock use and habitat variables produced few significant associations (Table 5). The number of broods using a habitat complex was correlated with earthworm abundance in both years and with the area of clearing and aspen in 1978. Although solitary birds correlated with area of clearing in 1978, this relation was not exhibited in 1979. None of the correlations between singing males and habitat variables were significant.

The potential impact of the different ground covers in the clearings on woodcock use was also evaluated. Numerical comparisons showed that 3 of 5 bare-ground, 1 of 12 rye grass, and 2 of 6 shrubby clearings were not used in 1978; each type of cover had one fewer unused habitat complex in 1979. These differences in use of clearings by singing males based on cover type were not statistically significant.

Table 3. *Correlations between woodcock use of the habitat complexes by year ($n = 23$).*

	Singing males		Solitary birds		Broods	
Woodcock use	1978	1979	1978	1979	1978	1979
Singing males						
1978	1.0					
1979	0.48*	1.0				
Solitary birds						
1978	0.25	0.23	1.0			
1979	0.50*	0.20	0.44*	1.0		
Broods						
1978	0.21	0.24	0.01	0.05	1.0	
1979	0.41	0.54*	0.16	0.25	0.20	1.0

*Significant at $P < 0.05$.

Table 4. *Average and range (in parentheses) of soil moisture and earthworm abundance and biomass for all habitat complexes (n = 23) by year.*

		Earthworms/0.25-m^2 plot	
Year	Soil moisture (%)	Number	Biomass (mg)
1978	12.5 (7.3–24.1)	2.67 (0–13.0)	540 (0–4,130)
1979	16.7 (9.7–32.1)	2.87 (0–17.2)	480 (0–4,070)

Table 5. *Correlations between woodcock use and habitat variables by year (n = 23).*

	Singing males		Broods		Solitary birds	
Habitat variables	1978	1979	1978	1979	1978	1979
Area of aspen habitat (ha)	0.30	-0.02	0.47[a]	0.17	0.26	0.06
Area of clearing (ha)	0.20	0.01	0.37[a]	-0.01	0.45[a]	0.17
Number of discrete openings	0.25	0.28	0.20	-0.11	-0.32	0.09
Shape of clearing	0.21	-0.27	0.11	-0.14	-0.09	0.16
Number of earthworms	0.19	0.29	0.35[a]	0.35[a]	-0.08	-0.06
Soil moisture	-0.07	-0.15	-0.19	0.07	-0.09	0.13

[a] Significant at $P < 0.10$.

Discussion

Male Woodcock

The high degree of fidelity to singing grounds by male woodcock that we observed is well documented (Sheldon 1967; Liscinsky 1972; Whitcomb 1974). The between-year correlation of singing males reported in this study ($r = 0.48$) would probably have been higher had it not been for the nine new singing grounds that were established in 1979 on seven habitat complexes. We have no data to indicate that these increases are the result of population changes in the area, nor can the increases be accounted for by a lag response to the clearings created in 1978.

Singing male woodcock adapt to a wide variety of vegetative structures in the clearings. Observations during the present study indicated that in the bare-ground and rye clearings, males had a tendency to select singing sites close to aspen edges, whereas in clearings with scattered shrubs, singing sites were located throughout the openings. Wishart and Bider (1976) believe shrubs offer predator protection for displaying males. In open fields, the proximity of singing sites to edges of clearings may be one way woodcock compensate for lack of shrubby cover. The greater association of singing males with the number of discrete openings versus the total area of clearings suggests that visual isolation is important in the selection of singing grounds. Wishart and Bider (1976) noted frequent aggression between territorial males not isolated by a structural barrier. Maxfield (1961) found that minimum size of a singing field was related to the height of surrounding vegetation.

The weak correlation between singing and solitary birds in both years, and the relatively small number of diurnal contacts, suggest that singing males in the present study often did not use adjacent aspen habitat as diurnal cover. In contrast, Mendall and Aldous (1943) and Sheldon (1967) documented numerous instances where diurnal cover was immediately adjacent to singing fields and males walked to courting sites.

Broods

Current methods for evaluating woodcock population trends are based on censuses of singing males (Artmann 1977) and depend on the assumption that the proportion of displaying males in the population is constant through time and under differing habitat conditions. Although support for the assumption is limited, the correlation we observed in 1979 between singing males and broods using the same habitat complex provides indirect supporting evidence. Lack of significance for the same correlation in 1978 was partly due to the smaller sample size. Additional supporting evidence has been reported by Whitcomb (1974), who found a correlation between the numbers of singing males and the total spring male population on High Island, Michigan, as derived from summer mist-net data over a five-year period. Because of the lack of sufficient field data to support the assumption that singing males are proportional to breeding population levels, Godfrey (1975) recommended abandoning singing-ground censuses in favor of other survey methods. Although singing-ground counts are an efficient means of censusing, additional research is needed to verify that a constant proportion of males in a population display, independent of changing habitat conditions and population density.

The association between woodcock use of habitat and earthworm abundance has long been suspected. Not until recently, however, has a strong dependency been demonstrated by Reynolds et al. (1977). The significant correlation between brood use and earthworm abundance found in our study supports their findings; male usage had a much weaker correlation to earthworm abundance. We suspect that when females are caring for broods, they spend a greater amount of time in feeding areas because of their necessarily restricted mobility.

The importance of earthworms in a habitat complex is further emphasized by the fact that the three habitat complexes never used by woodcock were devoid of earthworms, based on our sampling. The average number of earthworms per plot for habitat complexes used by woodcock in this study are in the same range as those reported by Reynolds et al. (1977) for woodcock habitat in Maine.

Management Considerations

Enough studies have been done on woodcock habitat preference so that we can begin to develop conceptual models to guide management practices. Habitat requirements of breeding woodcock can be grouped into three major components: food, diurnal cover, and singing grounds. By using the range of suitable conditions for each of these components as an indicator of their importance, we felt the following rankings to be appropriate:

Food > diurnal habitat > singing-ground habitat.

Also, since areas used as singing grounds are frequently used for summer roosting fields (Whitcomb 1972; Wishart and Bider 1976), the model probably can be applied to the postbreeding season as well.

Food habits analyses (Aldous 1939; Sperry 1940; Glasgow 1958; Dyer 1976) have shown that earthworms are the primary food in the woodcock diet. Reynolds (1977) found that only three species of earthworms are commonly eaten by woodcock. This high degree of specialization limits the woodcock to habitats that can support suitable and sufficient earthworm populations. Data from Reynolds et al. (1977) suggest that a strong association exists between community type and earthworm abundance because of differential palatability of the leaf litter, with aspen and alder being the most preferred species (Reynolds and Jordan 1975).

Diurnal habitat requirements are somewhat broader than food requirements. This conclusion is supported by the wide range of woodcock-associated vegetation types that have been reported (Sheldon 1967; Wenstrom 1973). More recently, structural analyses (Bourgeois 1977; Kroll and Whiting 1977; Rabe 1977) have suggested that understory features are better indicators of diurnal habitat suitability than species composition. Even from a structural standpoint, however, diurnal habitat requirements are fairly general.

Although the literature describes a variety of singing-ground habitats (Maxfield 1961; Sheldon 1967), studies have generally been unsuccessful in predicting their use on the basis of structural or species composition. Bennett et al. (this volume) found that adjacent diurnal communities were a better predictor of use than any feature within a clearing. Scattered shrubby fields seem to be preferred (Sheldon 1967), but woodcock will use practically any opening if there is enough area to take off and land. These data indicate that singing grounds have the most general requirements of the three components.

Our model suggests that selection of sites to be managed for woodcock should consider food availability as the top priority, then diurnal habitat, and finally the characteristics of the singing ground. Attempts to manipulate earthworm populations in the field would be unrealistic, yet habitats suitable for earthworms can easily be manipulated using normal forestry practices to produce desirable diurnal and singing-ground habitats for woodcock.

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Use of Longleaf Pine Stands by Woodcock in Southern Alabama Following Prescribed Burning

by

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Abstract

During the winters of 1979 and 1980, we compared the abundance of American woodcock (*Philohela minor*) among longleaf pine (*Pinus palustris*) stands in the Conecuh National Forest of south-central Alabama. Stands were grouped according to the length of time since their last prescribed burn. Three groups of stands were compared in 1979: those burned during the winter of study, and those burned 1 and 2 years before the study. Six groups of stands were compared in 1980: those burned during the winter of study; those burned 1, 2, 3, and 10 years before the study; and unburned control stands.

Woodcock abundance for both years was found to be significantly higher ($P \leq 0.05$) in stands burned during the winter of study than in stands burned 2 or more years before the study. In 1980 woodcock abundance was also significantly higher ($P \leq 0.05$) in stands burned 1 year before the winter of study than in those burned 2 or more years before the study.

Ground-cover density appeared to be the most important variable among the burned longleaf stands. Ground cover was very dense in stands burned 2 or more years before the winter of study (>80%), whereas in stands burned more recently, ground cover was <50%. Total soil invertebrate abundance did not differ among stands, regardless of time since the last prescribed burns.

Recent woodcock (*Philohela minor*) research in the Southeast has emphasized quantification of the habitat requirements of this species in attempts to develop practical management programs. Initial studies in Alabama have helped define the structural characteristics of diurnal and nocturnal habitat (Horton and Causey 1979) and of nesting habitat (Roboski 1979). To date, however, few studies have dealt with the impact of current land-management practices on this species.

Prescribed burning, a popular forest and wildlife management practice in the South, is frequently used in and around potential woodcock habitat in Alabama. Although nocturnal use by woodcock of burned areas has been reported (Glasgow 1958; Edwards and Ellis 1969; P. J. Mathews, unpublished data), no information is available on the effect of fire on diurnal habitat use.

The present study was conducted during the winters of 1979 and 1980 to evaluate the effect of prescribed burning on wintering woodcock in the Conecuh National Forest of southern Alabama. We compared diurnal woodcock abundance among stands of longleaf pine (*Pinus palustris*) that varied in the length of time since their last prescribed burn. Quantitative comparisons of vegetation structure (plant nomenclature follows Radford et al. 1968) and of the abundance of soil invertebrates were also made.

Study Areas

In 1979, work was conducted exclusively on the Conecuh National Forest (CNF). Additional areas located on the Solon Dixon Forestry Education Center (SDFEC) were included in 1980.

The CNF lies in the Middle Coastal Plain Province (Hodgkins et al. 1979) of extreme south

Alabama in Covington and Escambia counties. Topography is gently rolling to hilly and soils are deep, with sandy surface layers (Hajek et al. 1975). Upland wooded sites are dominated by longleaf pine, with open midstories composed primarily of flowering dogwood (*Cornus florida*) and longleaf pine. The most common understory plant is gallberry (*Ilex glabra*), and the most common ground cover species are wire grass (*Aristida stricta*) and broom sedge (*Andropogon* spp.).

The CNF is managed primarily for the production of longleaf pine sawtimber. Prescribed burning is used for competition control, site preparation, access improvement, hazardous fuel reduction, disease control, and wildlife habitat improvement. On the average, stands are burned once every 3 years during late fall and early winter.

The SDFEC is adjacent to CNF in northern Covington and Escambia counties and is maintained by Auburn University. We used unburned portions of the longleaf pine stands managed for turpentine production in this area as control stands. Trees in these stands averaged 45 years old and have always been protected from fire. Vegetation components, soil characteristics, and physiographic features were similar to those on the CNF.

Methods

Selection of Study Units

United States Forest Service records were used to group longleaf pine stands on the CNF according to the number of years since their last prescribed burn. Stands representing three burn groups were studied in 1979: those burned during the winter of study, and those burned 1 year and 2 years before the study. In 1980, stands representing six burn groups were studied: those burned during the winter of study, 1, 2, 3, and 10 years before the study, and stands on the SDFEC that had never been burned (control group). The average age of the trees in these stands was 40 ± 7 years; basal areas averaged 16 m^2/ha. Stands subjected to cutting or thinning operations within 12 months and grazed stands were excluded from study. In 1979, two stands in each burn group were selected for study. In 1980, three stands in each burn group were selected, with the exception of the 10-year-burn group, for which only two stands were available.

Census of Woodcock

Census of woodcock was conducted along 500-m line transects in each stand (two per stand in 1979, three per stand in 1980). Each transect was located by randomly selecting a starting coordinate corresponding .o 1-m increments along the boundary roads connecting two stands. Transects were oriented across contour lines to prevent land-feature bias, and no two transects were allowed to intersect.

Beginning in January of each study year, woodcock were counted along each transect, using a trained pointing dog. Four weekly censuses were made in 1979, six in 1980. The dog was allowed to hunt away from the transect only as far as he could be effectively controlled by the investigator. Birds pointed by the dog were flushed by the investigator and their direction of flight and landing spot noted to prevent recounting. The flush site was marked and the right-angle distance from the flush site to the transect line measured. Because these data were to be used as indices of comparison, the following formula (Leopold et al. 1951) was used to calculate the number of woodcock per hectare: woodcock/ha $= F \times 10{,}000/2L\bar{d}$, where F = number of woodcock flushed, L = length of the transect (m), and $\bar{d}$ = mean right-angle flush site distance (m). A least-squares analysis of variance was performed on these data, and the numbers of woodcock per hectare were compared among burn groups by Duncan's multiple-range test (alpha = 0.05).

Sampling of Soil Invertebrate Populations and Vegetation Structure

During the winter of 1980, soil invertebrate populations in each stand were sampled for comparison among burn groups. Each census transect was segmented and numbered, and a sample site was selected from a random numbers table. Cylindrical soil plugs (7.62 cm in diameter, 10.16 cm deep) were then removed from flush sites and random points along the transects in each stand. An attempt was made to take equal numbers of soil samples from flush sites and random sites each week in each stand. Invertebrates

Table 1. *Mean number of woodcock per hectare*[a,b] *(SEM given in parentheses) in longleaf pine stands that varied in length of time since their last prescribed burn, winter 1979 and 1980.*

	Length of time since last prescribed burn					
Year of study	Winter of study	1 year	2 years	3 years	10 years	Control
1979	0.55 x (0.19) N = 16[c]	0.08 xy (0.08) N = 16	0.01 y (0.01) N = 16	–	–	–
1980	0.26 x (0.04) N = 54	0.10 y (0.02) N = 54	0.04 z (0.01) N = 54	0.01 z (0.01) N = 54	0.04 z (0.01) N = 36	0 z N = 54

[a] Woodcock/ha = number of flushes × 10,000/2Ld, where L = length of transect (m) and d = mean right-angle flushing distance (m) from transect.

[b] Means on same line with a common letter are not significantly different ($P > 0.05$, Duncan's multiple-range test).

[c] N = number of censuses × number of transects.

were removed from soil samples in the field and placed in vials containing 10% formalin for preservation. Insect larvae were identified according to Peterson (1960, 1962).

The composition and structure of two vegetation strata in the stands were analyzed. Percent of ground covered by standing vegetation less than 0.3 m tall and percent of ground covered by leaf litter were visually estimated in 4-m² circular plots. Stem counts for vegetation more than 0.3 m tall but less than 2 m tall (shrub stratum) were also made in 4-m² circular plots. These plots were randomly located along each transect in each stand.

A least-squares analysis of variance was performed on invertebrate and vegetation data, and means were compared among burn groups by Duncan's multiple-range test (alpha = 0.05).

Results

Woodcock Use of Burned Stands

In 1979 and 1980, significantly more woodcock ($P \leq 0.05$) were found in stands burned during the winter of study than in stands burned 2 or more years before the study (Table 1). In 1980, significantly more woodcock were also found in stands burned 1 year before the winter of study than in stands burned 2 or more years before. No woodcock were found on any of the transects in the control stands. Systematic searches made in all control stands to verify the results of the transect censuses flushed only one woodcock.

On a few occasions, when stands burned the winter of study were being censused, a woodcock was known to have moved before being flushed. On these occasions the observation for that bird was omitted, resulting in negatively biased data for this burn group. We believe this did not cause a problem because it happened very infrequently, the number of woodcock in these stands was significantly greater than in the other burn groups in spite of this bias, and these data were used only as indices of comparison. This bias should be considered in future studies, however, because it could cause a problem in subsequent data analyses.

Soil Invertebrate Abundance

Soil invertebrate samples were taken from 61 flush sites and 80 random sites for comparison among burn groups. Specimens were found representing seven major invertebrate groups: earthworms (Annelida), centipedes (Chilopoda), snails (Gastropoda), spiders (Arachnida), and three insect orders: Coleoptera, Hymenoptera, and Diptera (Table 2). No significant difference ($P \leq 0.05$) was found in the total number of invertebrates among burn groups. Earthworms, recognized as a major woodcock food item (Sheldon 1967), were significantly less abundant in stands burned during the winter of study than in the 10-year stands. There were no differences in invertebrate abundance between samples taken randomly and those collected from flush sites.

Table 2. *Mean invertebrate abundance in soil samples*[a,b] *(SEM given in parentheses) in longleaf pine stands that varied in length of time since last prescribed burn, winter 1980.*

	Length of time since last prescribed burn					
Invertebrate group	Winter of study N = 36[c]	1 year N = 23	2 years N = 20	3 years N = 17	10 years N = 21	Control N = 24
Earthworm (Annelida)	0.44 y (1.46)	0.06 yz (0.31)	0.70 yz (0.36)	0.82 yz (0.27)	1.24 z (0.47)	1.00 yz (0.25)
Centipedes (Chilopoda)	0.08 y (0.05)	0.04 y (0.04)	0.20 y (0.12)	0.06 y (0.06)	0.05 y (0.05)	0.04 y (0.04)
Snails (Gastropoda)	0.06 y (0.06)	0.04 y (0.04)	0.05 y (0.05)	0.06 y (0.06)	0 y	0 y
Spiders (Arachnida)	0.06 y (0.04)	0.04 y (0.40)	0.05 y (0.05)	0 y	0 y	0 y
Coleoptera	0.14 y (0.07)	0.13 yz (0.07)	0 yz	0.06 yz (0.06)	0.10 yz (0.07)	0 z
Hymenoptera	0.08 y (0.05)	0 y	0.10 y (0.07)	0.18 y (0.18)	0 y	0.04 y (0.04)
Diptera	0.17 y (0.26)	0.04 y (0.04)	0 y	0.06 y (0.06)	0 y	0 y
Total	1.03 y (0.26)	0.91 y (0.30)	1.10 y (0.37)	1.24 y (0.40)	1.38 y (0.46)	1.08 y (0.25)

[a] Mean number of invertebrates per 7.62 × 10.16-cm cylindrical soil sample (463.3 cm^3).

[b] Means on the same line with a common letter are not significantly different ($P > 0.05$, Duncan's multiple-range test).

[c] N = number of soil samples.

Percent Ground Cover and Stem Densities

The most abundant plant species found in the ground vegetation stratum were wire grass, broom sedge, and seedling longleaf pine. Mean percent of ground covered by standing vegetation, leaf litter, total percent of ground cover, and total stem densities per hectare among burn groups are compared in Table 3. Mean percent of ground covered by standing vegetation did not differ significantly ($P \leq 0.05$) among burn groups.

The percent of ground covered by leaf litter differed significantly among burn groups (Table 3). Litter cover was significantly less ($P \leq 0.05$) in stands burned the winter of study (22%) and 1 year before the study (21%) than in stands burned 2 or more years before the study (>60%), where the thickness of leaf litter layers, primarily pine needles, exceeded 5.1 cm. Total percent of ground cover (percent standing vegetation + percent litter cover) was significantly greater ($P \leq 0.05$) in stands burned 2 or more years before the winter of study (>80%; Table 3).

The shrub vegetation stratum contained primarily gallberry, yaupon (*Ilex vomitoria*), wax myrtle (*Myrica cerifera*), longleaf pine, and *Vaccinium* sp. Stem densities were significantly lower ($P \leq 0.05$) in stands burned 1 year before the winter of study than in stands representing the other burn groups. This difference was apparently due to lower stem densities of gallberry, the most abundant species, which were approximately half those in stands representing the other burn groups.

Conclusions and Management Implications

The preference of woodcock for recently burned areas found in this study may have been the result of variation in the density of the ground-cover stratum caused by fire. Longwell (1951) noticed that woodcock preferred a minimum of ground cover, regardless of community type or density of the shrub cover in Pennsylvania. Liscinsky (1972) described optimum

Table 3. *Mean percent ground cover and mean stem*[a] *density per hectare*[b] *(SEM given in parentheses) in longleaf pine stands which varied in length of time since last prescribed burn, winter 1980.*

	Length of time since last prescribed burn					
	Winter of study N = 27[c]	1 year N = 27	2 years N = 27	3 years N = 27	10 years N = 18	Control N = 27
Mean % ground covered by standing vegetation	14.1 y	25.9 y	25.2 y	19.3 y	16.7 y	15.9 y
	(3.9)	(4.2)	(5.3)	(4.1)	(5.6)	(4.4)
Mean % ground covered by leaf litter	22.2 y	20.7 y	60.7 z	62.9 z	64.4 z	65.9 z
	(2.7)	(1.3)	(4.2)	(4.5)	(5.5)	(4.5)
Mean total % ground cover[d]	36.3 y	46.7 y	85.9 z	82.2 z	81.1 z	81.9 z
	(3.4)	(2.6)	(2.8)	(3.4)	(4.1)	(4.7)
Mean total stem density	27,675 y	17,000 z	26,000 y	28,050 y	25,550 y	32,150 y
	(3,[illegible]8)	(1,970)	(3,472)	(3,144)	(4,248)	(4,914)

[a] Vegetation > 0.3 m tall but < 2 m tall.

[b] Means on the same line with a common letter are not significantly different ($P > 0.05$, Duncan's multiple-range test).

[c] N = number of 4-m^2 plots sampled.

[d] Total % ground cover = % standing vegetation + % leaf litter.

woodcock habitat in Pennsylvania as having 25% ground cover. He concluded that ground cover that was too dense might hinder feeding activity, regardless of the available food supply.

Lambert and Barclay (1975) found that ground cover on frequently used sites in Oklahoma averaged 25%. Wishart and Bider (1976) concluded that ground cover in Quebec needed to be at least 70% clear of matted vegetation and litter. Horton and Causey (1979) found that the ground covered by standing vegetation averaged 47% in the diurnal habitat of woodcock in certain areas of Alabama.

All of these studies indicated that woodcock prefer fairly open ground-cover strata, 47% clear of vegetation. In the longleaf pine stands compared in the present study, the thick pine-litter layers that accumulate 2 or more years after burning and the standing vegetation at ground level may have deterred woodcock movements and feeding activity, even though the availability of potential food items was the same as in recently burned stands. In fact, soil conditions in the stands we studied appeared to provide favorable conditions for availability of earthworms to woodcock. Fayle (1961) reported that shallow-working earthworms thrive on acid soils, such as those associated with pine stands.

Another factor, which was not directly measured, may have been involved. Gallberry, the most abundant species in the shrub stratum, is an evergreen and has a dense foliage in the winter. In stands burned the winter of study, most of this foliage was removed by the fire, leaving naked stems. In stands burned 1 year before the study, only half as many gallberry stems were present as in other burn groups, and consequently, foliage attributed to this species was less dense. This factor or ground cover alone, or a combination of stem density, foliage density, and ground cover may have been important. Other investigators have suggested compensatory relations among structural components in woodcock habitat (Sheldon 1967; Horton and Causey 1979).

In summary, it appears that fire plays an important role by making an otherwise unsuitable habitat attractive to woodcock. Although the scope of this study limits the inferences to be drawn, we have observed diurnal woodcock concentrations on recently burned upland sites in other physiographic regions in Alabama. Similar studies in these regions are needed to broaden the knowledge of the effects of fire on woodcock habitat.

The effect of fire on nesting activity is another aspect which should be considered. Sizeable nesting woodcock populations have been found in Alabama (Causey et al. 1974; Roboski 1979). The characteristics of burned sites do not appear to be compatible with nesting requirements reported by Roboski (1979). We believe, however, that prescribed burning has definite potential as a woodcock habitat management tool, particularly in the Southeast.

Acknowledgments

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Serum Protein and Cholesterol Levels as Indicators of Reproductive Activity in Female American Woodcock Overwintering in Alabama

by

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Abstract

Seventy female American woodcock (*Philohela minor* Gmelin) were collected throughout Alabama from 10 December 1976 to 24 February 1977. Ovary weight and ovarian follicle diameter, levels of serum cholesterol and total serum protein, and the relation between these two blood variables and follicle development were measured. Means for ovary weight and follicle diameter for February were higher ($P<0.05$) than during December and January. The mean levels of serum cholesterol and total serum protein for February were higher ($P<0.05$) than those for December but not for January ($P>0.05$). The positive correlations between total serum protein and follicle diameter ($r = 0.77$), serum cholesterol and follicle diameter ($r = 0.80$), and total serum protein and serum cholesterol ($r = 0.90$) for February were higher ($P<0.05$) than the respective correlations ($r = 0.28$, $r = 0.47$, and $r = 0.29$) for the December–January period. The present investigation indicated that some female woodcock were beginning sexual recrudescence while others remained quiescent during the "overwintering" period in Alabama. We suggest that total serum protein and serum cholesterol levels may be used as indices of female woodcock reproductive status, enabling separation of breeding from nonbreeding living birds in the field.

Little literature exists concerning the reproductive physiology of the American Woodcock (*Philohela minor* Gmelin), especially regarding breeding on the traditional "wintering" grounds. Recent investigations by Causey et al. (1974) and Ammann (1975), and observations by the authors indicate that breeding by woodcock overwintering in Alabama is more intense and consistent than previously reported (Imhoff 1962; Sheldon 1971), but that not all female woodcock become sexually active before spring migration. It would be desirable to know what portion of the overwintering population actually breeds and nests on the wintering areas.

Variations in blood constituents are often indicative of the reproductive status of vertebrates (van Thienhoven 1961); the present investigation was therefore initiated to define the range of specific blood constituents of the female woodcock and to determine their relations to ovarian growth and follicle maturation during vitellogenesis. The use of such data, taken from a random collection of woodcock, may enable identification of the southern breeders.

Increases in total serum protein levels parallel increases in serum estrogen levels during the breeding season in the domestic turkey (*Meleagris gallopavo gallopavo*) (Mukherjee et al. 1969) and in the eastern wild turkey (*M. g. silvestris*) (Martin 1976). Bell and McIndoe (1962) reported that plasma protein levels of the domestic hen (*Gallus domesticus*) peaked during the 10-day period preceding egg laying. Sturkie (1965) reported that serum cholesterol levels also increase as a function of serum estrogens and may be used as an indicator of ovarian follicle development and sexual recrudescence. Stammeler et al. (1955) reported noticeable elevations in plasma cholesterol levels of domestic chickens to which estrogens were administered.

Our objective in the present study was to develop a simple technique for distinguishing breeding from nonbreeding female woodcock as an indication of their reproductive status in Alabama without the necessity of killing any birds. We planned to accomplish this by quantifying levels of total serum protein and serum cholesterol of female woodcock for a period preceding and including the peak breeding season in Alabama and correlating these values with ovarian follicle development.

Methods

Representative counties from the major physiographic regions of Alabama were randomly selected as collection areas. Sites that appeared to be favorable woodcock habitat were located, systematically searched with trained pointing dogs, and the woodcock flushed and shot.

Secondary wing feather characteristics were used to age woodcock (Martin 1964). Specimens were separated into hatching year (HY) and after hatching year (AHY) age classes, with one modification: birds collected after 1 January 1977 that still had HY plumage were classified as HY birds.

Birds were collected from 10 December 1976 through 24 February 1977. One of three methods was used to collect blood in 3-mL plastic vials. With birds not yet dead from gunshot, the right jugular vein was incised and the blood collected. With dead birds, either the neck was severed and the blood obtained from the jugular vein, or the thoracic cavity was opened, the major arteries and veins severed, the heart massaged, and the blood collected. All blood samples and woodcock carcasses were preserved in ice until they were taken to the laboratory for processing.

Blood samples were centrifuged for 20 min at 2,000 *g* and the serum removed and frozen in stoppered glass vials at − 10° C until analysis. The left ovary was removed, cleaned of excess tissue, fixed in 10% formalin for 1 week, and transferred to 70% ethanol. After 1 week, each ovary was blotted and weighed to the nearest 0.01 mg. The diameter of the largest ovarian follicle was measured to the nearest 0.1 mm.

Total serum protein levels were measured colorimetrically by a modification of the biuret method, using an Accu-Stat blood chemistry analyzer (Clay-Adams Co., Parsippany, N.J.). A 30-μL serum sample from each bird was analyzed in duplicate and the mean value recorded. A few samples, contaminated by hemolysis, were corrected in the following manner. The percent hemoglobin in each sample was determined by sodium dodecyl sulfate (SDS) polyacrylamide gel electrophoresis (Jovin et al. 1964). The gels were prepared according to Laemmeli (1970), and the percent hemoglobin in each contaminated serum sample was subtracted from the total serum protein values obtained with the Accu-Stat analyzer.

Serum cholesterol levels were determined colorimetrically, using an Accu-Stat analyzer in a modification of the Lieberman–Burchard method. Duplicate 30-μL samples were measured for each woodcock and the mean value recorded.

Monthly means for all variables were calculated and analyzed by using the F-max test and analysis of variance. Analysis of variance was also used to determine if significant differences existed between the two age classes within and among months for all variables. When significant differences were found, Duncan's multiple-range test was used to locate these differences.

All variables were plotted against each other and against time and were tested visually for linearity for the following periods: the nonbreeding portion of the collection period (10 December 1976–31 January 1977), the breeding portion (1–24 February 1977), and the entire collection period. A sample correlation coefficient analysis was performed for all variables for the same intervals. The correlation coefficients for the breeding and nonbreeding periods were tested for equality of correlation according to Morrison (1976). The level of significance in all statistical procedures was accepted as being $P \leq 0.05$ (unless otherwise indicated). All statistical procedures were processed by using the statistical analysis system (SAS) of Barr and Goodnight (1976).

Results

Variable Analysis

In all, 70 ovaries and 53 serum samples were collected. Mean ovary weights increased during the collection period (Fig. 1). Mean ovary weights (mg) for December (39.5 ± 14.5), January (84.66 ± 13.8), and February (193.26 ± 13.0) differed. There were no differences between ovary weights for HY and AHY age classes, either within or among months.

Mean ovarian follicle diameters increased

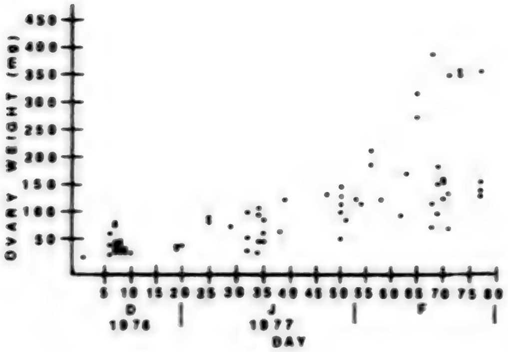

Fig. 1. Left ovary weights of individual female American woodcock.

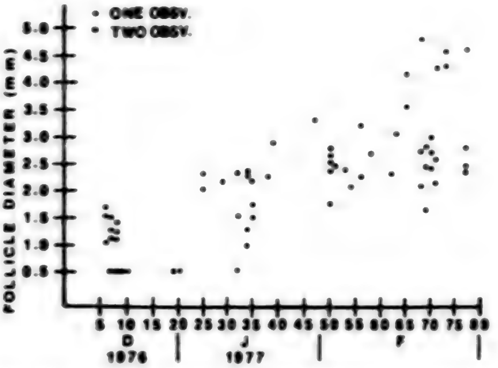

Fig. 2. Diameter of the largest ovarian follicle of individual female American woodcock.

from December through February (Fig. 2). Mean follicle diameters (mm) for December (0.8 ± 0.16), January (2.1 ± 0.15), and February (3.0 ± 0.14) differed. The mean follicle diameters for HY and AHY age classes were not different within or among months.

Mean total serum protein levels (g/dL) showed increases from mid-January through February (Fig. 3). The mean total serum protein level for December (4.51 ± 0.32) was lower than that for February (5.55 ± 0.24), but not different from that for January (5.18 ± 0.31). There were no differences in total serum protein levels between HY and AHY age-class woodcock, either within or among months.

Increases in serum cholesterol levels (mg/dL) are apparent in the mid-January through February sample (Fig. 4). The mean cholesterol level for December (188.86 ± 10.1) was lower than that for January (237.70 ± 9.7) and February (245.04 ± 7.7). The mean levels for January and February were not different, and there were no differences between HY and AHY age classes within or among months.

Correlation Analysis

The relations among total serum protein, serum cholesterol, follicle diameter, and ovary weight are evident from the positive correlations among these variables for the entire collection period (Table 1). However, greater positive correlations are evident when the breeding and nonbreeding portions of the collection period are compared (Table 1). The correlation ($r = 0.77$, $P < 0.01$) between total serum protein and follicle

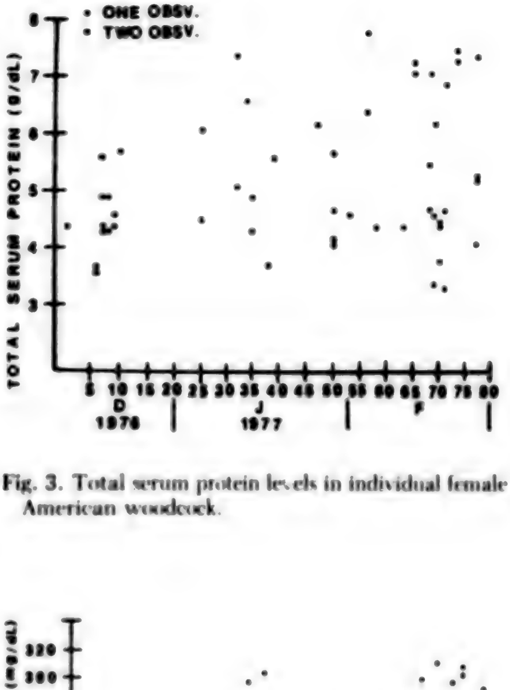

Fig. 3. Total serum protein levels in individual female American woodcock.

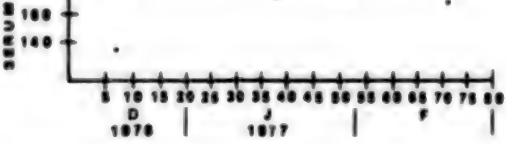

Fig. 4. Serum cholesterol levels in individual female American woodcock.

Table 1. *Sample correlation coefficients for ovary weight, follicle diameter, total serum protein, and serum cholesterol for female American woodcock for the nonbreeding period (10 December 1976–31 January 1977), the breeding period (1–24 February 1977), and the entire collection period (10 December 1976–24 February 1977).*

	Correlation coefficients		
Variable[a]	1	2	3
Nonbreeding period			
1. Ovary weight			
2. Follicle diameter	0.86* (44)[b]		
3. Total serum protein	0.24 (29)	0.28 (29)	
4. Serum cholesterol	0.25 (29)	0.47**(29)	0.29 (29)
Breeding period			
1. Ovary weight			
2. Follicle diameter	0.95**(26)[b]		
3. Total serum protein	0.80**(24)	0.77**(24)	
4. Serum cholesterol	0.85**(24)	0.80**(24)	0.90**(24)
Entire collection period			
1. Ovary weight			
2. Follicle diameter	0.90**(70)[b]		
3. Total serum protein	0.65**(53)	0.58**(53)	
4. Serum cholesterol	0.67**(53)	0.69**(53)	0.66**(53)

[a] Variable numbers on vertical and horizontal lines correspond.

[b] Numbers in parentheses represent sample sizes.

*$P < 0.05$.

**$P < 0.01$.

diameter during the February breeding period was greater than for the December-January nonbreeding period ($r = 0.28$, $P < 0.15$). The correlation ($r = 0.80$, $P < 0.01$) between serum cholesterol and follicle diameter for February also was greater than for the December–January period ($r = 0.47$, $P < 0.01$). The correlation ($r = 0.90$, $P < 0.01$) between total serum protein and serum cholesterol during February was greater than during the December–January period ($r = 0.29$, $P < 0.10$).

The relation between follicle growth and changes in blood chemistry during sexual recrudescence is illustrated by the following additional correlations. Follicle diameter ($r = 0.95$, $P < 0.01$), total serum protein ($r = 0.80$, $P < 0.01$), and serum cholesterol ($r = 0.85$, $P < 0.01$) were positively correlated with ovary weight during February (Table 1). These correlations were greater than the respective correlations ($r = 0.86$, $P < 0.05$; $r = 0.24$, $P < 0.10$; $r = 0.25$, $P < 0.15$) for the December–January period.

Interpretation and Conclusions

During February, some female woodcock were becoming sexually active while others remained quiescent (Figs. 1, 2). The positive correlations among the measured variables during February (Table 1) support this observation. The positive correlation ($r = 0.95$, $P < 0.01$) between ovary weight and follicle diameter during February agrees with the study of Hutchinson et al. (1968) on the domestic canary. They reported a linear relation between ovary and follicle growth, with follicle size as the more reliable indicator of the initiation of the breeding season.

February is normally the peak breeding month for woodcock in Alabama (Causey et al. 1974). The increased mean total serum protein level for February suggests that some females were undergoing physiological changes associated with the onset of sexual activity. Sturkie (1976) reported increased serum protein levels during vitellogenesis. Vanstone et al. (1955) reported that the serum protein levels of the domestic fowl increased just before egg laying, decreased during laying, and recovered upon cessation of laying. Sendroy et al. (1961), and Heald and Badman (1963) reported a similar prelaying rise in plasma proteins in the pigeon (*Columba livia*).

Increases are expected in serum cholesterol levels from mid-January through February, during the period of egg yolk formation (McIndoe 1971). Martin (1976) reported that plasma cholesterol levels in the female eastern wild turkey rose sharply at the beginning of the breeding season and declined smoothly throughout the remainder of the breeding season.

The positive correlations ($P<0.01$) among ovary weight, follicle diameter, total serum protein, and serum cholesterol for February, and the higher means for these variables during February, were primarily influenced by the values of eight individual woodcock (Figs. 1, 2, 3, 4). Although statistical comparisons were not possible, these eight birds had the greatest values of all woodcock examined during February for the variables measured. These higher values would be expected in birds entering the rapid, final stage of vitellogenesis.

Because no ovarian follicles were found that appeared to be nearing the end of the final phase of growth as described by Marza and Marza (1935), it was not possible to determine peak values for the variables measured. There were six follicles with diameters greater than 4.0 mm; the largest follicle was 4.8 mm in diameter, and the ovary from which it was taken weighed 388.01 mg. Extrapolation from the work of Gilbert (1971) on the domestic fowl suggests that these woodcock would have just entered the final period of rapid follicle growth, with about 7 to 14 days until ovulation. After the present study was completed, we collected a female woodcock with a fully developed ovary and a recently ovulated ovum. The ovary weighed 8.22 g, and the ovum was 23 mm in diameter. This finding indicates that in the woodcock a massive accumulation of yolk material occurs in the last phase of follicle growth before ovulation and is in agreement with the study of Stamps and Doerr (1977) on woodcock reproduction in North Carolina.

According to Marshall (1961), cold temperature is an inhibitor of the reproductive cycle in many temperate-zone avian species. In an increasingly cold environment, the effects of a lengthening photoperiod are nullified and reproduction is delayed. The average maximum temperature (6.8° C) for January 1977 at Auburn, Alabama, was 7.1 degrees lower than the 30-year average. The average minimum temperature (−4.3° C) was 5.9 degrees lower, and the mean temperature (1.3° C) was 6.4 degrees below average. Therefore, temperature was likely a factor in the delayed sexual recrudescence in many of the female woodcock that would normally have been sexually active.

Although female woodcock with fully mature follicles were not collected, the significantly positive correlations among the measured variables during February indicate that fluctuations of total serum protein and serum cholesterol levels can be used as indices of the reproductive status of the female woodcock. From the available data, we speculate that any female woodcock with total serum protein levels greater than 6.3 g/dL and serum cholesterol levels greater than 295 mg/dL is sexually active and is approaching the final rapid phase of ovarian maturation. However, further investigations are needed to determine the values of the blood variables during the entire final phase of follicle development.

The lower correlations among the variables for the entire collection period (Table 1) support the premise that not all females become sexually active on the Alabama "wintering" grounds. That none of the variables were positively correlated ($P>0.05$) with time during February indicates that the variables were not increasing for all woodcock examined. The use of the specific blood variables should make it possible to distinguish sexually active female woodcock from quiescent ones.

After the present study was completed, we kept a captive group of 12 woodcock for a period of 8 weeks and modified a blood collection technique described by McClure and Cedno (1955). We were able to collect 1 mL of blood from the right jugular vein of each woodcock on a weekly basis without any adverse effects. Therefore, further research to determine the values of the blood constituents during the complete reproductive cycle will enable the use of this technique with living birds and permit the capture, blood collection, and release of woodcock in the field.

We believe that this means of identifying reproductively active woodcock, in conjunction with further investigations of woodcock reproduction in Alabama, will enable us to arrive at an estimate of the relative numbers of woodcock that nest in Alabama. The contribution that Alabama breeders are making to the continental population should be further investigated. Differentiation of breeders from nonbreeders should be helpful in determining whether implementation of management practices for the establishment and maintenance of suitable breeding and nesting habitat is justifiable. It should also help in estimating the effectiveness of such practices. Expansion of the data collection to include woodcock from throughout the southern portion of their range could lead to a more precise understanding of the reproductive biology of the species.

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Breeding Biology of American Woodcock in East Texas

by

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Abstract

During the winters of 1978–80, we counted courtship flights of male American woodcock (*Philohela minor*). Woodcock were collected from mid-November to early March during the wintering periods of 1977–78 and 1978–79 and during the 1979–80 hunting season. Birds were aged and weighed, and the length of the left testis or diameter of the largest ovarian follicle was measured.

Males initiated regular courtship flights about 1 January in all three years. Frequency of flights showed a bimodal curve each year. In all cases, the second peak, presumably caused by an influx of northward moving migrants, was higher.

Testes lengths ranged from 3.0 to 12.0 mm, with a significant ($P \leq 0.05$) difference in lengths of adults and subadults. Correlation coefficients of length over time were significant for both age classes, and intercepts were significantly different between age classes. Testes recrudescence began about 7 December in adults and about 21 December in subadults. All males collected after mid-February were sexually mature.

Follicle diameters of adult and subadult females were significantly different ($P \leq 0.05$). Correlations of follicle diameter with time were significant in both age classes; coefficients, intercepts, and slopes were significantly different between age classes. Onset of follicle recrudescence began about 1 January in both age classes. Follicle diameter was significantly correlated to bird weight in adults only, indicating that weight is a factor in breeding readiness of adult hens. The nine hens collected with follicles in the rapid eruption stage were adults; this suggests that only adult hens nest in East Texas. Nest initiation dates ranged from early February to mid-March.

American woodcock (*Philohela minor*) are winter residents of forested areas in East Texas. Cruickshank (1968) noted that males regularly perform courtship flights on warm winter evenings in East Texas; a small portion of the area is considered nesting range of the species (Owen 1977). Davis (1961) reported nests near College Station; more recently, Pulich (1978) and Cain et al. (1978) recorded nests and a brood in the area. In other southern environs, Causey et al. (1974), Stamps and Doerr (1977), and Roberts and Dimmick (1978) noted sizable late-winter breeding populations in Alabama, North Carolina, and Tennessee, respectively. Conversely, Pace and Wood (1979) found little evidence of woodcock nesting in coastal South Carolina.

In East Texas, we investigated the (1) chronology of male courtship behavior, (2) onset and degree of gonadal recrudescence in both sexes, and (3) frequency of nesting by females. Although we recognize that the term recrudescence does not definitively describe gonadal enlargement of birds that have not previously attained the breeding condition, we will use it in this way.

The Data

Displaying Males

During the winters of 1977–80, from three to six observers counted courtship flights of male woodcock. Forestry and biology students at Stephen F. Austin State University assisted in the counts. Each observer was given a short training period, then allowed to select a courting site and

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time period, either morning or evening, for censusing. All fields censused were pine plantations ranging in age from 0 (site prepared but not planted) to 6 years old. Each observer recorded the number of courtship flights heard at the selected site. Censusing started about 20 January and ended about 15 March, or after two clear census days when no courting birds were heard. Each observer averaged at least two census days per week. To eliminate bias caused by traffic noise, differences in observer acuity, and temporary inaccessibility of some fields due to impassable roads, we grouped the data by 5-day periods. We then computed average number of courtship flights per observer day during that period and divided by the total number of flights for the year to obtain a weighted percent per 5-day period.

Gonadal Recrudescence and Nesting

Using trained bird dogs, we collected woodcock during the 1977–80 hunting seasons. We also collected birds after the hunting season until early March in 1978 and 1979. Collecting was discontinued each year after two hunting days when no birds were located. No birds were collected after the hunting season in 1980. We did not collect any birds in or immediately adjacent to courtship fields.

We weighed specimens to the nearest 1.0 g and separated them into adult or subadult age classes (Martin 1964). Birds hatched the previous spring were classified as subadults, all others as adults. We measured, to the nearest 0.5 mm, length of the left testis for males or diameter of the largest ovarian follicle for females. In 1979, for females with follicles in the rapid eruption stage (Stamps and Doerr 1977), we measured diameters of all maturing ovarian follicles. When an ovulating female was collected, we searched the flush area for a nest.

Statistics

We used student's *t*-tests to compare gonad size of mature and subadult birds of the same sex. Within each sex and age class, we tested the relation of gonad size to collection date and body weight using simple linear regression. With one exception (adult hens), neither transformations of gonad sizes nor multiple regressions of gonad size with date and weight improved the regression value more than 0.10. For each sex, we tested regression values, slopes, and intercepts between age classes using confidence intervals and equations in Dixon and Massey (1969). In all cases, we used a null hypothesis of no difference between groups being tested and a significance level of 0.05.

Displaying Males

We recorded 757 courtship flights in 1978, 1,136 in 1979, and 984 in 1980. The earliest flight recorded was 16 December 1979; birds did not initiate regular flights until after about 1 January. No flights were observed after 15 March. Because courtship flights continue later in the spring in more northern areas (Sheldon 1967), we assume that all courting males had migrated north by then.

During all three years, peak numbers of flights occurred between 13 and 27 February (Fig. 1); these dates are similar to those noted in Louisiana (Sheldon 1967). Peak numbers of flights in Oklahoma occurred between 10 and 20 February 1975 and 1976 (Barclay and Smith 1977) and between 5 and 12 March 1978 in Tennessee (Roberts and Dimmick 1978). In both States, displaying males were still present about 2 weeks later than in Texas. Sheldon (1967) reported that peak courtship flight activity occurred as late as mid-May in Maine, Massachusetts, and Michigan; regular flights generally ceased about 1 June. These data show that male American woodcock perform regular courtship flights in some parts of their range over a 5-month period. period.

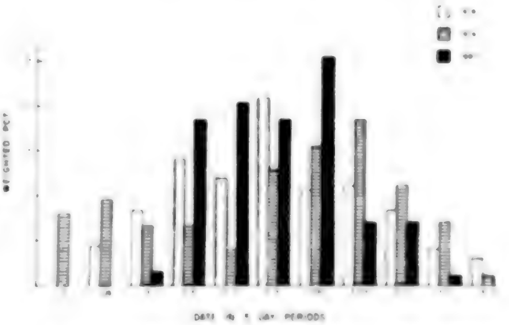

Fig. 1. Nuptial flights grouped by 5-day periods during 1978, 1979, and 1980. Date shown is the third day of the period.

The numbers of courtship flights showed a minor peak followed by a major peak each year (Fig. 1). Other researchers have noted similar trends (Sheldon 1967; Barclay and Smith 1977; Couture and Bourgeois 1977). Sheldon (1967) hypothesized that in Massachusetts the second peak was related to renesting attempts. Couture and Bourgeois (1977) showed that in Quebec the first and highest peak was a result of the passage of migrants, and the second peak was caused by resident males. Boggus and Whiting (unpublished data) recorded relatively more courting males in brushy stands 6 years old than in grassy stands 0 to 2 years old early in the winter courtship period; later in the season, this trend was reversed. We suspect winter resident birds inhabiting the brushy stands constituted the early peak and that the second peak was a result of some movement by winter residents to grassy areas, combined with an influx of northern-moving migrants. If so, grassy stands might serve as staging areas; we wonder if courtship flights play a role in initiation of northward migration.

Gonadal Recrudescence

We collected 142 woodcock in 1977–78, 176 in 1978–79, and 32 in 1979–80. There were 174 males (99 adults, 65 subadults, and 10 of unknown age) and 176 females (100 adults, 55 subadults, and 21 of unknown age). One setting female and three males performing courtship flights were collected.

Males

Testes Length

If the testes of a collected bird were dark colored, we assumed recrudescence had not yet begun (Anthony and Buss 1974). Lengths of quiescent testes ranged from 3.0 to 4.0 mm; those of mature birds were slightly longer than those of subadults. Average length of the left testis in adults was 7.19 mm; those of subadults averaged 6.28 mm. The difference between the age classes was significant. Blanchard (1941), Johnston (1956), and others have shown differences in testes lengths of adults and subadults in several other avian species.

Testes lengths of the three woodcock collected while performing courtship flights illustrate the large degree of overlap between age groups. A subadult, collected 16 February 1978, had a longer testis (10.5 mm) than either of two adults (both 8.0 mm) collected 24 February 1978 and 30 January 1979. Johnson (1961) noted similar conditions in mallards (*Anas platyrhynchos*).

Testes Recrudescence

Regression values. – The regressions of testis length with bird weight were not significant for either adult or subadult birds. However, regressions of testis length with collection date were significant for both age classes (Table 1). These values demonstrate that testis recrudescence in adult and subadult males was very similar. Were it not for the different intercepts, a single prediction equation could be used for both age classes. Differences in intercepts show recrudescence of subadults lagged about 14 days behind that of adults. Similar differences have been noted in other species (Wright and Wright 1944; Johnston 1956).

Table 1. *Values in the regressions of left testis length with collection date for adult and subadult male woodcock and comparisons between the two age classes.*

Value	Adult	Subadult	Comparison
R	0.715	0.754	Nonsignificant
R^2	0.511	0.569	Not compared
Intercept	3.16	2.16	Significant
Slope	0.069	0.069	Nonsignificant
No. cases	92	61	Not compared
F ratio	94.2	78.6	Not compared

Using 9-day periods, Stamps and Doerr (1977) developed a regression equation for length of left testis with collection date for 19 birds collected between 6 December and 1 February 1975–76 in North Carolina. Their slope (0.053 mm/day; P. Doerr, personal communication) and correlation coefficient (0.693) values were similar to ours (Table 1). Their intercept (4.24 mm) was much higher than ours, probably a result of the shorter collection period.

Chronology of testes recrudescence. – Some researchers have noted that lengthening of the photoperiod stimulates testes recrudescence (Blanchard 1941; Sturkie 1965; Jones 1978).

Testes recrudescence of collected birds began about 7 and 21 December in adult and subadult males, respectively. These dates are similar to those noted by Stamps and Doerr (1977) for woodcock and Allen and Perry (1979) for mottled ducks (*Anas fulvigula*). As testes recrudescence of the birds we collected began before the winter solstice, we do not believe that lengthening photoperiod is the primary factor triggering that response. Several factors, including warm temperatures (Roberts and Dimmick 1978), cold temperatures (Blanchard 1941), and photoperiod length (Dang and Guraya 1978), are probably as important as the lengthening photoperiod.

Testes lengths varied widely throughout January in adults and into mid-February in subadults (Fig. 2). Blanchard (1941) noted similar size discrepancies in white-crowned sparrows (*Zonotrichia leucophrys*) collected in California. Johnson (1961) hypothesized that the length of time a bird has been territorial will affect testis size. We believe this to be the cause of the large variation we noted. During early January, some birds were initiating regular courtship flights; others did not start until later in the month. By early February, testes lengths of all adults and most subadults exceeded 7.0 mm. During this period, the relative number of courtship flights increased markedly (Fig. 1). By mid-to-late February, when we noted maximum courtship activity, testes of all birds collected were 8.0 mm or longer. Thus we believe regular courtship activity begins when length of the longer testis exceeds about 7.0 mm. Roberts and Dimmick (1978) reported that male reproductive maturation is complete by mid-February; our results support this conclusion.

Females

Diameter of Ovarian Follicles

If a bird had several ovarian follicles of the same size, we assumed recrudescence had not yet begun (March and Sadleir 1970). Quiescent follicles ranged from 0.5 to 2.5 mm in diameter (Fig. 3). Most quiescent follicles in adults were 2.0 mm in diameter; those in subadults were 0.5 mm. Diameters of the largest follicles in adult birds averaged 3.47 mm; those in subadults averaged 2.00 mm. These values were significantly different.

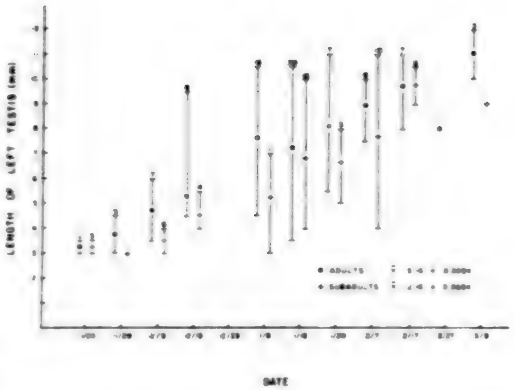

Fig. 2. Average and ranges of left testis lengths grouped by 10-day periods. Date shown is the fifth day. Numbers above range limits show sample sizes.

In subadult mallard hens, Johnson (1961) noted that follicles began enlargement early in the fall and reached the size of mature hens by late November. Our data on woodcock show different trends. None of the five adult hens with follicles 0.5 mm in diameter were collected after 16 December. Fifteen of the subadults had follicles of that diameter; nine were collected after that date, the last on 21 January. Similarly, there was little overlap between follicle diameters of adult and subadult birds until early January. Finally, in no subadult bird collected during the study period was the follicle diameter greater than 4.0 mm.

Recrudescence of Ovarian Follicles

Regression values.—Linear regressions of ovarian follicle diameter with collection date

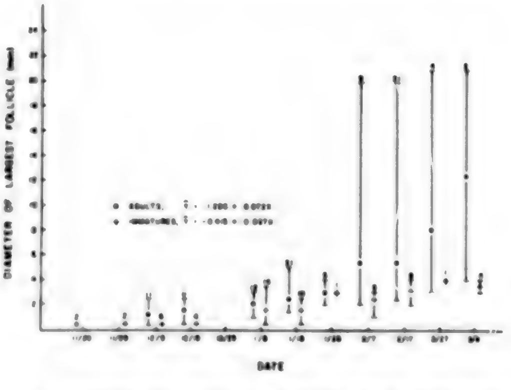

Fig. 3. Average and ranges of ovarian follicle diameters grouped by 10-day periods. Date shown is the fifth day. Numbers above range limits show sample sizes.

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Table 2. *Values in the regressions of diameter of the largest ovarian follicle with collection date for adult and subadult female woodcock and comparisons between the two age classes.*

Value	Adult	Subadult	Comparison
R	0.459	0.814	Significant
R^2	0.245	0.662	Not compared
Intercept	-1.200	-0.415	Not compared
Slope	0.072	0.037	Significant
No. cases	98	55	Not compared
F ratio	31.2	104.2	Not compared

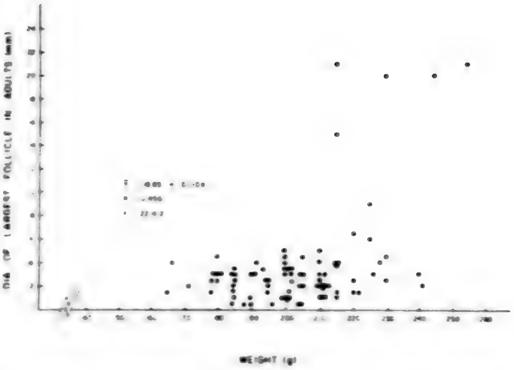

Fig. 4. Diameter of largest ovarian follicle of adult females as related to bird weight.

were significant for both age classes (Table 2). However, due to lack of variation in follicle diameters in subadult females, the correlation coefficient for that age class was much higher than for adult females.

In a population having a rapid eruption stage, one would expect data transformation to increase the correlation coefficient (J. Howard, personal communication). With $\log_{10}$ transformations, coefficients increased from 0.459 to 0.741 for adults and from 0.814 to 0.827 for subadults. The large increase for adults shows that ovarian follicles of some birds had entered the rapid eruption stage (Fig. 3). Conversely, lack of change for subadults demonstrates that none of the collected birds had entered that stage. This finding suggests that only adult females reach breeding readiness in East Texas.

Adult females were the only group in which gonad size was significantly related to bird weight (R = 0.456, F = 22.4, N = 87; Fig. 4). The same was true for the multiple regression of adult follicle diameter with collection date and weight (R = 0.618, F = 25.9). Diameter of the largest follicle is thus positively related to weight in adult females. This relation indicates that there is a minimum base weight which adult females must reach before they are ready to lay. Our data suggest this base weight is around 210 g. It is noteworthy that the nesting hen weighed 215 g.

Chronology of follicular recrudescence.—Ovarian follicles of both adults and subadults began slow recrudescence about 1 January, 2–3 weeks after the onset of male testes recrudescence. Kirkpatrick (1944) reported similar finds for ring-necked pheasant (*Phasianus colchicus*), as did Johnson (1961) for mallards, and Blanchard (1941) for white-crowned sparrows.

Rapid maturation of ovarian follicles takes place after follicle diameter exceeds 4.0 mm (Stamps and Doerr 1977) or 5.0 mm (Roberts and Dimmick 1978). Our data do little to help define this critical diameter. Follicle diameters (in mm) of three ovulating birds were (dashes indicate ruptured follicles):

(1) 9.0, 7.0, 5.0, 5.0, 4.0, 4.0, 3.0;
(2) 15.0, 11.0, 6.0, 5.0, 5.0, 4.0, 4.0, 4.0, 3.0;
(3) 21.0, 19.0, 15.0, –, –, 3.0.

Our earliest evidence of rapidly maturing follicles was in a bird collected 5 February 1978 that had a shelled egg in the oviduct. Of the adult hens collected after 1 February, 20% (8 of 39) had ovarian follicles exceeding 5.0 mm, and 38% (15 of 39) exceeded 4.0 mm. Two of four adult hens collected during March had shelled eggs in the oviduct. Although we excluded subadult females, our February percentages are lower than those of Stamps and Doerr (1977) in North Carolina and Roberts and Dimmick (1978) in Tennessee.

Nesting Females

We recorded one nest and six broods. Eleven chicks from five of the broods were aged using bill length (Ammann 1974). Additionally, while quail hunting on 2 February 1980, our dog captured an adult female woodcock on an empty nest. External examination of the cloaca indicated that the bird was approaching oviposition. Characteristics of the nests and broods are given in Table 3.

These data demonstrate that nest initiation

Table 3. *Some characteristics of woodcock nests and broods found in East Texas during 1979 and 1980.*

Date located	Number of Chicks	Number of Eggs	Approximate chick age (days)	Approximate clutch completion date
1979				
9 March	2		10	7 February
9 March	1		5	11 February
9 March	4		1	15 February
10 March		4	–	10 March
1980				
2 February		0	–	6 February
1 March	2		3	6 February
25 March	2		8	25 February
12 April	4		"small"	mid-March

dates varied widely from early February to mid-March, a period of about 6 weeks. Causey et al. (1974) noted similar February dates in Alabama, but none in March, thus indicating a shorter nesting period. In North Carolina, Stamps and Doerr (1977) recorded clutch completion dates that ranged from late January to early April. A wide variation is thus evident in clutch completion dates of woodcock that nest in the South.

Conclusions

Our results indicate that physiological and physical breeding activity in American woodcock is common on East Texas wintering grounds. Testes recrudescence starts in early December, and regular courtship flights begin about 1 January. By mid-February, when courtship activity peaks, virtually all males have reached sexual maturity. Adults attain that condition about 2 weeks earlier than subadults.

Recrudescence of ovarian follicles starts about 1 January. Some adult hens reach sexual maturity by late January; we noted three hens that had started nesting by the first week in February. We believe that a sizable number of adult hens nest in East Texas, but we found no evidence of subadult hens nesting in the area.

The extent of woodcock breeding and nesting in East Texas clearly needs further investigation. Some hens probably breed in the area but nest farther north. Thus quality and quantity of courtship grounds may be of major importance. We have information on neither the number of birds that nest locally nor their habitat requirements. Land managers need such information for proper integration of woodcock into their forest resource management plans.

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Woodcock Use of Agricultural Fields in Coastal North Carolina[1]

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Abstract

We studied the use of agricultural fields in North Carolina by American woodcock (*Philohela minor*) each year from 1975 to 1978 during November through March. Captures of 1,184 woodcock were made during this period. Immature males represented 41% of the banded sample. Adult males, females, and immature females were equally represented. Of the recoveries of banded woodcock, 80% (16 of 20) indicated points of origin in northeastern North America. Results of density comparisons for roosting birds in four types of agricultural fields indicated a strong preference for untilled soybean fields over fields with untilled and rebedded corn; woodcock were never observed in fields planted with winter wheat. Using nearest-neighbor measurements, we found that woodcock aggregated in small clusters within the banding fields. This behavioral trait may be of importance for woodcock in alarming "neighbors" of the presence of predators.

Numerous investigations have been undertaken to explain the crepuscular flights of woodcock (*Philohela minor*) from diurnal coverts to nocturnal fields. It has been suggested that open fields may serve as roost sites (Krohn 1970) and facilitate escape from predators (Dunford and Owen 1973). Along migration routes and at wintering grounds, these fields may provide important feeding habitat for woodcock (Britt 1971; Dyer and Hamilton 1974; Krohn et al. 1977). The variability in the characteristics of fields used at night by woodcock throughout their range (Glasgow 1958; Krohn 1970; Krohn et al. 1977; Britt 1971; Wishart 1973; Dyer and Hamilton 1974, Hale and Gregg 1976; Horton 1976) presumably reflects the regional variability of agricultural practices, which to a large extent determines the availability of different types of fields. Increased knowledge of the selectivity displayed by roost-searching woodcock when presented with a variety of agricultural field types might lead to an increase in banding efficiency by concentrating search efforts on choice roost fields (Owen 1974). As Krohn (1970) aptly stated, the "knowledge of why woodcock use openings at night might permit more effective banding if these areas could be modified to attract woodcock."

In the present paper we report on woodcock banded during three consecutive years (1975 to 1978) on the Coastal Plain of North Carolina. The rates at which woodcock were observed and the efficiency with which they were captured are discussed. Comparisons of the vegetative and structural components of specific roost sites and observations of selection among types of agricultural fields by roost-searching woodcock on the

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Coastal Plain and on a selected Piedmont floodplain are also reported. Further, the pattern of woodcock distribution on selected roost fields is analyzed and discussed.

Study Area

In the Coastal Plain region, banding operations and roost-field censuses were undertaken in fields located near the community of New Holland in southern Hyde County. This area supports farming operations in which corn and soybeans are the principal crops. It is a common agricultural practice in this area to disk corn and soybean stubble after harvest in November before sowing winter wheat; however, many harvested soybean and corn fields remain structurally intact throughout the winter until farming operations resume in early March. Most fields are bordered by swamp thickets, hardwood bottomlands, and pine plantations, which serve as diurnal cover for woodcock. A more detailed description of the area is given by Stamps and Doerr (1976).

Stamps and Doerr (1976) reported that woodcock were found most frequently in untilled soybean fields and, in the present study, our principal banding effort targeted this field type. However, intensive searches for roosting birds were conducted during 14 regularly scheduled banding nights on other field types that lay adjacent to the soybean banding fields, including tilled and untilled cornfields, cornfields that had been harrowed and sown in winter wheat, and tilled soybean fields. Since the corn and soybean crops were rotated annually, our banding and census efforts were shifted accordingly. Densities of roosting woodcock on the various field types were then compared. Searches for woodcock in other types of field were conducted simultaneously with soybean field banding efforts if sufficient personnel were available; otherwise, these efforts were conducted immediately before the soybean field banding efforts.

In the Piedmont, an experimental nocturnal habitat study was implemented at the New Hope Valley game lands, about 4 km southwest of Wilsonville in Chatham County. We chose 4 ha near the center of a 26-ha abandoned field as the study plot. Further details of the vegetation and adjacent diurnal habitat characteristics were reported by Stamps and Doerr (1976).

On the New Hope study plot, a randomized complete block design (Cochran and Cox 1957) was used to test woodcock roosting preferences in four types of managed fields. During the 1976–77 winter season, field types included prescribed burn, strip-disked, completely disked, and control vegetation plots. These field types were modified for the 1977–78 season to incorporate a "bare" row-furrow structural complex by bedding those plots which had previously been completely disked. Further, the previously strip-disked plots were simply "mowed" the second season.

Each 0.25-ha prescription plot at New Hope was randomly located in each of four blocks so that each block included one of each type of plot. Thus 16 prescription plots, totaling 4 ha, were monitored for roosting woodcock. Numbers of woodcock were determined by using nightlighting and flush counts during 14 census periods in February and March 1977 and 8 census periods from December 1977 until early March 1978. Variability in percent ground cover and soil moisture among the plots was also recorded.

Data collected at New Hope were not considered to conform to independent event theory, since there were relatively few observations per night and the probability of encountering repeating individuals was high. Data were analyzed according to the probability that each prescription type of plot was equally attractive to woodcock, and departure from this model constituted nonrandom selection.

Capture Methods

Woodcock were located in the study areas by using head-mounted nightlights and were captured with long-handled nets (Glasgow 1958) during 59 banding attempts over three winter seasons (November through March, 1975–78) (Table 1). Age and sex for each captured bird were determined by plumage characteristics (Martin 1964). Records were kept of the field location, the approximate number of woodcock observed, the incidence of capture, and the total man-hours expended.

Search procedure on each banding field consisted of a pair of workers traversing a line perpendicular to cultivation rows. Woodcock were consistently found in the furrows between the row mounds. Although banding experience

Table 1. *Comparison of capture efficiency, observation per man-hour, capture per man-hour, and density levels for woodcock on banding fields at New Holland, North Carolina, 1975–78.*

Season	Total man-hour effort	Total observations	Total captures	Mean Obs/hour	Mean cap/hour	Density[a]	Efficiency (%)
1975-76[b]	241 (17)[c]	705	356	2.93	1.45	–[d]	50.4
1976-77	260.5 (22)	949	416	3.64	1.59	2.83	43.8
1977-78	213.5 (20)	1,165	412	5.45	1.92	3.05	35.3
Totals[e]	715 (238)	2,819 (963)	1,184 (395)	3.94	1.65	–	42.0

[a] Total observations/hectare surveyed.

[b] Data from Stamps and Doerr (1976).

[c] Number of banding night periods.

[d] No data available.

[e] Means given in parentheses.

varied and close supervision was necessary for some novices, no attempt was made to quantify the disparity of success for efforts by inexperienced and experienced banders. To reduce the disturbance to roosting woodcock, we did not reenter a banding field during the same week (Owen and Morgan 1975).

Measurement of Spacing

During the banding, it was frequently noted that while the observer was approaching one bird, another, perhaps one or two rows away, would flush. To investigate the spatial distribution of woodcock roosting on these fields, we used the nearest-neighbor method (Clark and Evans 1954). Miller and Stephen (1966) similarly applied this model to determine spatial relations in flocks of sandhill cranes. This method has the distinct advantage of eliminating the effect of the size of a quadrat by measuring only the distance between individual members of the population. Still, as Clark and Evans (1954) pointed out, the boundaries of space must be "chosen with care" when computing the density measure.

At New Holland, woodcock were found almost exclusively within the boundaries of untilled soybean fields; furthermore, they were apt to be found at any location within a field that provided reasonable access and proximity to diurnal cover. The low, flattened terrain of Hyde County, with its high water table, necessitates the use of drainage ditches to enable the sustained growth of crops. We believed that the drainage-ditch borders of the soybean fields which were sampled would serve as "natural" boundaries for density calculation, if no other soybean fields were continuous with their boundaries.

The pattern of spacing for roosting birds on New Holland soybean fields was measured during banding operations on two occasions in February 1977 and on five occasions during January 1978. Painted stakes were placed at each observation site, whether or not a capture was made. If a bird was flushed prematurely, a stake was placed near its perceived roost site and relocated to the nearest woodcock splash mark on the following day. Distances to the field borders and the nearest neighboring roost site were recorded. Measurements of furrow depth, soybean stubble height, and soil conditions were also recorded on two occasions and were compared with similar measures taken at random locations in these same fields.

Banding Results

Woodcock Captures

We encountered 2,819 woodcock during the three winter seasons and captured 1,184 (Table 1). Age–sex composition of the banded sample remained relatively constant from year to year. Immature males represented an average of 41% of all banded birds; adult males, adult females, and immature females were equally represented. Although the number of woodcock observed and captured per man-hour of effort increased during the three seasons, there was a simultaneous decrease in the efficiency of capture.

Observations of woodcock varied markedly from November through early March, and means of 2.83 and 3.05/ha were recorded during the 1976–77 and 1977–78 seasons, respectively (Table 1). Observation rates varied significantly ($R^2 = 0.78$) when regressed with seasons ($P<0.05$, F test) and months ($P<0.001$, F test); however, these rates and the numbers of birds observed per hectare were highly variable within and across banding fields throughout each season. Fewer birds than 2/ha were located during 40 and 20% of the banding nights in the 1976–77 and 1977–78 seasons, respectively. In those seasons, 4/ha or more were observed during 31 and 25% of the surveys. The largest numbers of birds recorded were on 24 February 1977 and on 8 January 1978, when 10.8 and 10.5 woodcock per hectare were observed in 7.3-ha and 5.8-ha soybean fields, respectively.

Woodcock banded during the winter at New Holland apparently summer and migrate in the eastern flyway region (Krohn and Clark 1977; Wishart 1977; Coon et al. 1978). Twenty individuals banded at New Holland were reported killed as of 15 May 1980, for a recovery rate of 1.8%; of these, 16 were from the northeastern United States and Canada. Three recoveries were spring-found birds from New Hampshire (4 April 1978), Nova Scotia (24 May 1978), and Pennsylvania (4 April 1978). Of four North Carolina recoveries, one was found in the spring (13 May 1978). Hunter-killed birds were reported from Ontario (1), Quebec (2), Maine (2), New Hampshire (1), New York (4), New Jersey (2), and Massachusetts (1). These recovery records strongly suggest that the breeding-ground origin of our wintering population is centered in the northeastern region of North America.

Most migrants arrive in North Carolina in mid-December and remain until mid-February to early March, depending on the prevailing weather conditions. Age and sex composition data, which indicate a preponderance of immature males in the captured sample, are consistent with the reports of banders at numerous migration and wintering concentration sites (Martin et al. 1969; Rieffenberger and Ferrigno 1970; Britt 1971; Krohn et al. 1977).

Recaptures

A total of 70 woodcock banded at New Holland were recaptured on or near the fields of their original capture; 54 of these were classified as repeats (netted again the same season they were banded), and 16 were designated as returns (netted in a season subsequent to banding) (Table 2). Two of the returns were caught two seasons after their banding. No data were available from the 1975–76 season.

More than 70% of the repeats occurred in the field of original capture (Table 2) after a mean interval of 3.2 weeks. No relation was found between the elapsed time (in days) and the distance between netting sites for repeat captures. Of 12 returning birds, 3 were renetted in or on fields adjacent to those of their banding; the other 9 returns were taken within 0.8 km of the original banding site. Thus, recapture and repeat records

Table 2. *Percent of woodcock recaptures and repeats occurring at original banding sites near New Holland, North Carolina, 1976–78.*

	1976–77				1977–78			
	Repeats[a]		Recaptures[b]		Repeats		Recaptures	
Location	No.	%	No.	%	No.	%	No.	%
Identical field	12	60	2	33	27	84	1	17
Less than 0.8 km	19	95	6	100	32	94	3	50
Less than 1.6 km	19	95	6	100	34	100	3	50
Less than 3.2 km	19	95	6	100	34	100	4	67
Greater than 3.2 km	1	5	–	–	–	–	2	33
Unknown	–	–	3	–	–	–	1	–
Total	20		9		34		7	

[a] Refers to woodcock which were renetted in the season in which they were banded, after a mean interval of 3.2 weeks.

[b] Refers to woodcock which were renetted in seasons subsequent to their banding.

indicate that at least some New Holland woodcock overwinter in the area and return in subsequent winters, often homing to the identical fields in which they had been banded. Glasgow (1958) and Britt (1971) have reported similar homing tendencies for woodcock wintering in Louisiana.

Spacing Patterns of Woodcock

There were no significant differences in the measurements of soybean stubble height taken at 55 random locations and 53 roost-site locations on two soybean fields totaling 21 ha ($P<0.57$, F test). Similarly, there were no differences in the depth of the furrows at the same random-and roost-site locations. There was no evidence that woodcock select roost sites in a soybean field on the basis of the height of residual soybean stubble or the depth of the intact row or furrow.

The frequency distribution of individual distances (distance to nearest neighbor) for 238 woodcock whose roost sites were marked in five different fields on seven sampling nights is illustrated in Fig. 1. The mean distance (±SD) to nearest neighbor was 19.04 ± 16.39 m (range, 0 to 97 m), and 50% of the roost sites were located within 5 m of another (Fig. 1). These distance measures become important when considered in terms of the field area and the density of birds on each field.

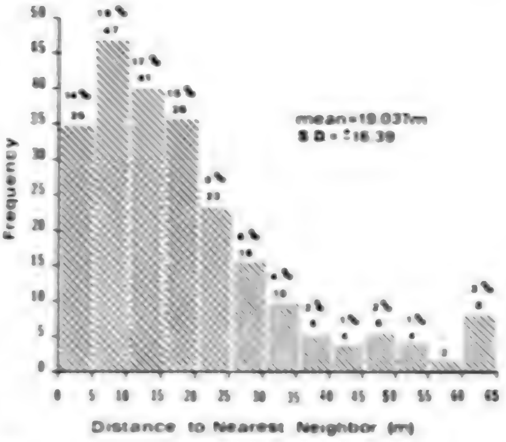

Fig. 1. Frequency distribution for the distance to nearest-neighbor for 238 woodcock located on roost sites at New Holland, North Carolina.

In each of the fields studied, roost sites were not spaced in a random fashion, but rather showed signs of significant aggregation (Table 3). This tendency to aggregate was frequently observed in fields where small, loosely spaced groups of birds (two to four individuals)

Table 3. *Measurements of spacing for woodcock in soybean fields that served as roost sites in the coastal plain of North Carolina.*

Date	Field	Area (ha)	Total no. of birds	Density (no./m^2)	$\bar{r}_A$ (m)	$\bar{r}_E$ (m)	R	$\sigma_{\bar{r}_E}$	C^e
1977									
17 February	1	7.28	26	0.0003	23.10^a	32.58^b	0.70^c	11.10^d	-2.79**^{e}
18 February	2	10.79	27	0.0002	25.54	31.90	0.80	10.43	-1.98*
1978									
8 January	3	5.82	53	0.0009	10.51	16.67	0.63	1.24	-4.95**
11 January	4	21.32	40	0.0001	27.00	37.50	0.72	13.06	-2.86**
12 January	5	9.67	27	0.0002	13.75	50.75	0.27	3.73	-9.91**
27 January	6	7.84	29	0.0003	19.65	33.33	0.58	2.90	-4.71**
18 February	7	5.82	36	0.0006	16.25	25.00	0.65	1.86	-4.70**

[a] Mean of observed distances (meters) to nearest neighbor.

[b] Mean distance (meters) to nearest neighbor expected in an infinitely large random density.

[c] $R = \bar{r}_A/\bar{r}_E$ = departure from randomness; greater than 1 approaches regular spacing, less than 1 approaches clustered spacing.

[d] Standard error of the mean distance to the nearest neighbor in a randomly distributed population of the same density as that of the observed; $\sigma_{\bar{r}_E} = 0.26136/\sqrt{Np}$, where N = no. of distance measurements, p = density observed.

[e] Significance test of departure from randomness; $C = (\bar{r}_A - \bar{r}_E)/\sigma_{\bar{r}_E}$; *significant at 5% level; ** significant at 1% level.

Table 4. *Comparison of field-type usage by roosting woodcock during census periods in the 1977-78 banding season at New Holland, North Carolina.*

Agricultural field type	Total area censused (ha)	Density of woodcock (mean no./ha)
Untilled soy stubble	108.4 (14)[a]	3.378 (365)[b]
Untilled corn stubble	79.28 (7)	0.202 (16)
Corn field; rebedded	29.29 (4)	0.034 (1)
Winter wheat	49.86 (7)	0.0 (0)

[a]Number of census periods in which field-type was checked.
[b]Total number of woodcock observed.

were spotted or flushed. These clusters were normally scattered throughout the field area, and only rarely was the distribution of woodcock roosts noticeably skewed to one section of a field.

Roost-Field Preferences

Coastal Plain Observations

The densities of roosting woodcock were about 16 times higher on untilled soybean fields than in untilled cornfields and about 100 times higher than in rebedded cornfields (Table 4). Woodcock were never observed to roost in fields of winter wheat.

These findings are made more dramatic by comparing them with examples of recorded densities on fields in which crop burdens were rotated between seasons. In a 10.8-ha soybean field, woodcock densities averaged 2.50/ha during six observation periods in 1976–77; during one census in 1978, this field, then in untilled corn, harbored only 0.47 woodcock/ha. Similarly, a 7.3-ha soybean field searched in 1976–77, which had averaged 3.47 woodcock/ha (six observation periods), was searched twice in 1978, when it was in untilled corn, and averaged only 0.48 woodcock/ha. An adjacent 11.2-ha untilled soybean field, unchecked the previous year while planted in corn, averaged 2.71 woodcock/ha during three periods in 1978. Thus it seems woodcock select untilled soybean fields for feeding and roost sites in preference to other field openings available at New Holland.

Manipulation of Nocturnal Habitat in the Piedmont

Thirty-two woodcock were recorded during 14 observation periods at New Hope [illegible]. Of these, 26 were found in burned plots and 6 were in control plots. Strip-disked and completely disked plots were never used by woodcock.

Although not more than three woodcock were sighted on any night, it is noteworthy that they were found only in the burn and control type of plots. If the plot selection was purely random for each bird, this seems intuitively unlikely. If for each block we consider only the nights with maximum number of birds, we find:

		Burn	Disk	Strip	Control
Block 1	either	3	0	0	0
	or	2	0	0	1
Block 2	either	2	0	0	0
	or	1	0	0	1
Block 3		1	0	0	0

Woodcock were never observed in Block 4; therefore, this block was not included in our calculations.

The probability for all arrangements at least as apparently nonrandom as these was calculated to be 6/64 = 0.094. This calculation was done on the assumption that birds seen the same night are, in fact, different individuals. Further, under the hypothesis of purely random selection, birds would have a probability of one in four of selecting any one of the four treatments. The calculation allows for the fact that the exclusive use of any other pair of treatments (i.e., other than burn and control) would have been regarded as equally nonrandom.

Although this calculation used only the nights with maximum number of individuals, the site selections on other nights are in complete agreement with the data used in this analysis and could only lend additional support to the conclusions.

Percent coverage of vegetation on the prescribed burn plots was consistently sparser than that on the control vegetation plots. Little vegetation remained on the completely disked plots, and stripping provided alternately dense and sparse cover. Soils were generally moist or frozen throughout the area, although pools of standing water were present on two blocks. Of additional interest was the observation that woodcock were almost always found roosting in old furrows of this fallow farm field (31 of 32 observations). Disruption of the row-furrow complex, excessive exposure of soils, and the denuding of protective vegetation on the plots that were completely disked and on the strip-disked plots might explain the dearth of roosting woodcock in those areas.

Results of the 1978 census were limited by an inadequate sample (only six of eight attempts produced observational records), due in part to an inundation of the study area as a result of heavy rains in early March. Thus, no statistical inferences can be made. However, woodcock were again found most often in burned areas (15 of 25 observations), but they were also present in modest numbers on the strip areas (6 of 25 observations) that had been mowed rather than disked before the 1978 season, and on control plots (4 of 25 observations).

Discussion

Spacing exerts more influence on the success of capture attempts than does the density of woodcock in the field. Glasgow (1958) noted that in Louisiana, woodcock appeared to cluster in sections of fields and that capture success was less when the spacing of birds decreased to less than 15.2 m. Krohn (1971) and Wishart and Bider (1976) reported that woodcock distribution on summer fields was not random but appeared to be more local and aggregated. Rieffenberger and Ferrigno (1970) termed these neighboring birds "eyewitnesses" to capture attempts.

The nature of, and stimulus for, this aggregating tendency have not been fully explored. Horton and Causey (1974) found that, after completing crepuscular courtship activity, male woodcock would abandon their singing grounds to aggregate with other woodcock on concentration areas in the same field. Suspecting that food availability might vary among or within fields, Ensminger (1954) measured earthworm populations throughout used and unused fields but found no differences. Krohn (1970) found that little food was obtained on summer fields, and Dunford and Owen (1974) speculated that these fields may provide protection from predators and serve as roost sites.

At New Holland, many of the captured woodcock had fresh mud on their bills. At times, movements of earthworms, snails, and other invertebrates were observed on these fields, and we suspected that woodcock were feeding during the night, as reported in Louisiana (Glasgow 1958; Britt 1971). Still there were no differences in the structural characteristics of soybean stubble or furrow depth within the fields, and the wide distribution of woodcock clusters and the field homogeneity make it seem unlikely that roosting birds would aggregate within a field section solely for its vegetative protection or its invertebrate resource.

Krohn et al. (1977) reported seeing singles and small groups of woodcock alighting on Cape May banding fields at various times during the night, and attributed this to migrant arrivals. Crepuscular abandonment of diurnal cover by one woodcock may trigger others to follow, so that woodcock would enter roost fields in small groups. This behavioral trait alone may explain the aggregations found.

From our observations, we suspect that the relatively close spacing of individuals within a group provides an alarm system within each cluster because when one bird flushes, the neighboring birds are alerted to approaching danger. For the bander, the implications of an "alarm" system are evident. Each individual bird sighting should therefore be checked for neighboring birds and an approach strategy developed before a capture attempt is made.

Agricultural Field Selection

Many investigators have described the types of fields in which woodcock have been found roosting. In Louisiana, woodcock have been located in pastures, fallow fields, and in cultivated corn, cotton, and sugar cane fields (Glasgow 1958). More recently in Louisiana, soybeans have become a dominant agricultural crop used for roost sites by woodcock (Martin et al. 1977). Krohn et al. (1977) found woodcock in abandoned fields, lightly grazed pastures, and alfalfa fields; heavily grazed pastures were avoided. Rieffenberger and Ferrigno (1970) reported use of similar field types but added that woodcock were rarely found in fields which had been sown with rye or a winter cover crop.

At New Holland, untilled soybean fields supported the largest number of roosting or feeding woodcock; fields that had been disked or planted in cover crops were never used. Glasgow (1958) also found little use of tilled land by woodcock. The selection of the untilled soybean rather than corn fields may be due to its moderate-to-sparse vegetative character, which provides a high degree of "protected" visibility. The soybeans also contribute nitrogen to the soil, which may influence invertebrate populations. Finally, the texture and color of the duff in soybean fields may be of importance in maintaining unfrozen soil beneath it and may provide an added measure of protective coloration in comparison with the lighter duff in corn furrows.

Row-Furrow Complex

In censusing woodcock both at New Holland and at New Hope, one striking similarity was observed in the use of agricultural fields by woodcock. Roosting birds were most frequently found in the furrows between rows. It is certain that protection from both predators and harsh weather is afforded roosting birds by settling between two mounds of earth. Perhaps the furrow also allows a measure of access by woodcock to food sources that would not be available if the terrain were flat. We frequently observed frozen soil on the tops of row mounds, while the soil under the duff in the furrow remained unfrozen. If earthworms or other invertebrate food sources move to depths of 30 cm or more during periods of freezing temperatures, then the average furrow depth of 23 cm, with its unfrozen soil, might provide access to an otherwise unavailable food source. The potential for using the row-furrow complex as an attractant for woodcock remains to be investigated.

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Effects of Habitat Variables on Foraging of American Woodcock Wintering in East Texas

by

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Abstract

Between mid-December 1979 and March 1980, we conducted a study in the southern portion of Nacogdoches County, Texas, to characterize preferred feeding sites of American woodcock (*Philohela minor*) in young pine plantations. Habitat use was evaluated by using flush counts along transects and probe-hole counts on clipped plots of 1 m radius, and on four 2- × 10-m belt transects radiating from each plot. Multivariate regression showed that vegetation characteristics were more important in influencing foraging activities than were soil characteristics. Significant ($P \leq 0.05$) factors included foliage densities at two levels, heights of mid-story woody species, soil moisture, soil pH, and percent of ground cover. Use of the major soil types of the area differed significantly, with both vegetation and soil characteristics influencing site selection.

Although the piney woods of East Texas lie within the western extremes of American woodcock wintering range, little information is available concerning the biology or management of the species in Texas. Leopold (1933) pointed out the value of studying a species on the periphery of its range, but a search of the technical literature revealed only six publications on woodcock in Texas. Only one of these (Kroll and Whiting 1977) presented results of a research project.

In other southern areas, bottomlands have been the subject of most winter habitat studies (Glasgow 1958; Sheldon 1967; Britt 1971; Fenwood 1976); few authorities mention the use of upland sites (Sheldon 1967). Kroll and Whiting (1977) and Whiting (1978) discussed the importance of young upland pine plantations in East Texas as habitat for wintering woodcock. To further define habitat features important to woodcock wintering in such stands, our study was designed to (1) identify soil types and characteristics and vegetation variables important to woodcock wintering in young upland pine plantations, and (2) correlate soil type and habitat variables with foraging activities of the birds.

Methods

Description of Study Area

We selected an upland pine-hardwood tract located in Nacogdoches County, 9 km west of Chireno, Texas, for study. Except for buffer strips along creeks, the tract was clearcut during 1972 and 1976. Residual vegetation was then sheared and debris raked into windrows that were not burned. The area was machine planted to loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) in 1973 and 1977.

Vegetation on the study area was typical of early successional upland sites in East Texas. In addition to loblolly and shortleaf pine, commonly occurring woody species included sweetgum (*Liquidambar styraciflua*), southern red oak (*Quercus falcata*), smooth sumac (*Rhus glabra*), shining sumac (*Rhus copallina*), southern wax-myrtle (*Myrica cerifera*), and a variety of other woody species. Other vegetation consisted of vine and herbaceous species such as greenbriars (*Smilax* spp.), Carolina jessamine (*Gelsemium sempervirens*), and dewberry (*Rubus* spp.). Major grasses included pinehill bluestem (*Andropogon divergens*) and beaked panicum (*Panicum lanuginosum*).

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Using unpublished U.S. Soil Conservation Service soil maps, we selected four major soil types: Bowie and Kirvin, both fine sandy loams, and Lilbert and Tenaha, both loamy fine sands. Within each soil type we established three transects, each 300 m long (thus a total of 12 transects for all soil types). Each transect was divided into 100-m intervals, and 2 circular plots each with a radius of 1 m were randomly located in each interval, resulting in 6 plots per transect, 18 per soil type, and a total of 72 plots. Vegetation was clipped and removed from each plot, and overhanging branches from adjacent trees and shrubs were removed to create foraging sites.

Estimates of Woodcock Use

Each week from 26 December 1979 to 28 February 1980, we censused each transect with a close-ranging bird dog and recorded the number of woodcock flushed per transect (Reid and Goodrum 1957). We began censusing 30 min after sunrise and completed six transects per day. When possible, all were completed within two consecutive days to decrease weather effects. We rotated the order in which we censused transects each week to reduce biases due to time of day and dog fatigue.

During the weekly census, we also counted woodcock probe holes within each clipped plot and in four belt transects, each 2 m wide and 10 m long, radiating from the plot. Direction of one belt transect at each plot was randomly established before every count. The other three transects were then set at 90° intervals (Fig. 1). Probe holes were obliterated after every count. All soil types were completely censused, including probe-hole counts, nine times during the study.

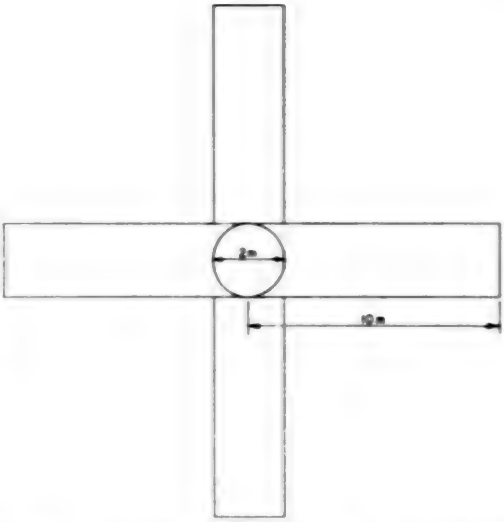

Fig. 1. A schematic diagram of a study plot and its associated belt transects.

Soil Analyses

Soil samples were taken weekly at randomly selected points within each plot. In the field, samples were placed in aluminum containers with secure lids to avoid mixing soils or loss of moisture by evaporation. In the laboratory, we used the gravimetric method (Gardner 1965) to measure soil moisture of each plot for each observation period. Soil samples were then stored in separate containers by plot. At the end of the study period, for each plot, percent gravel was determined by weight, texture (i.e., percent sand, silt, and clay) was evaluated using the Bouyoucos method (USDA Soil Conservation Service 1972), and pH was measured with a pH meter, precise to 0.1.

Habitat Analyses

Woody vegetation (>25 cm tall) around each plot was characterized by counting the numbers of individuals per woody species on four 4-m^2 subplots randomly established 8 m from plot center. From these data we computed plant species diversity (Shannon 1948). Percent ground cover (<25 cm tall), categorized as soil, litter, grass, herb, or woody, was determined on two 10-point transect lines adjacent to each plot. A foliage density index (FDI) was obtained by estimating the percentage of a graduated board, 10 cm high and 60 cm long, that was obscured and by dividing that percent by observer-to-board distance (MacArthur and MacArthur 1961). Maximum observer-to-board distance was set at 15 m. We determined FDI's for the following five vegetation strata: 0.00–0.25 m, 0.26–0.75 m, 0.76–1.25 m, 1.26–2.00 m, and 2.01–3.00 m.

Statistical Analyses

We performed statistical comparisons using the *Statistical Package for the Social Sciences*

(Nie et al. 1975) and *Biomedical Computer Programs: P Series* (Dixon et al. 1977). A total of 20 independent variables were tested for possible effects on the foraging activity of woodcock. Stepwise multiple regressions were used to select variables that significantly influenced the numbers and distribution of probe holes within the study area. Multivariate regression was then used to determine which of these variables had the greatest effect on foraging by the birds. One-way analysis of variance and Duncan's multiple-range tests were used to test and define differences in numbers of probe holes and differences in soil and vegetation characteristics of the soil types. Significance levels of 0.05 were used throughout the study.

Results and Discussion

The winter of 1979–80 was one of the mildest in recent years for East Texas and resulted in diminished populations of wintering woodcock. Flush data collected were insufficient for analyses; our results are therefore based entirely on probe-hole data.

Habitat Factors Affecting Woodcock Foraging

Vegetation

Foliage density. – The importance of understory vegetation cover to woodcock habitat has been emphasized by several authors (Glasgow 1958; Wenstrom 1974; Lambert and Barclay 1975; Fenwood 1976; Rabe 1977). In the multivariate equation, we found that foliage density at two heights explained the largest amount of variation in probe-hole numbers (Table 1). Density from 0.00–0.25 m had the greatest effect on forage site selection, with the number of probe holes increasing as foliage density decreased. The inverse relationship occurred in the density stratum at 0.26–0.75 m, with the number of probe holes increasing as density increased. Feeding behavior of woodcock and reduced risk of predation offer the best explanations for these results. Sparse vegetation cover at ground level increased mobility and visibility, and dense vegetation at the higher stratum provided the protection requirements of the habitat.

Table 1. *Significant multivariate regression values, using soil, vegetation, and ground cover as independent variables and average numbers of probe holes per plot and belt transects as dependent variables* ($\alpha = 0.05$).

Independent variables[a]	R	R^2	F ratio
Vegetation			
FDI[b] 0.00–0.25 m	0.713	0.509	8.16
FDI 0.26–0.75 m	0.643	0.414	5.56
Average height (m) of dominant vegetation	0.679	0.461	6.74
Soil			
Moisture (average)	0.585	0.342	4.10
pH	0.476	0.227	2.32
Ground cover (%)			
Bare soil	0.540	0.292	3.25
Litter	0.676	0.457	6.63

[a] Variables tested for which no significance was demonstrated include soil type; percent sand, silt, clay, and gravel in the soil; percent grass, herb, and woody in the ground cover; FDI in the strata at 0.76–1.25 m, 1.26–2.00 m, and 2.01–3.00 m; and plant species diversity.

[b] FDI = foliage density index.

Average height of dominant species. – Fenwood (1976) used shrub heights (0.9–6.4 m) as an aid in classifying woodcock habitat in southern West Virginia as good, fair, or poor. In our study, heights of dominant woody species ($\bar{X}$ = 3.2 m, range = 1.8 to 4.7 m) proved significant in influencing feeding by woodcock; the number of probe holes increased with vegetation heights (Table 1). This type cover best fits the mid-story vegetation described by Britt (1971) as vertical cover with erect and spreading life forms. However, since differences in probe-hole numbers were not significantly related to plant species diversity, we agree with Britt (1971) that it is the structure of the habitat, not its composition, that is important to the birds. In southern pine plantations, this type of habitat should continue to be favorable for woodcock use until canopy closure affects understory vegetation or significantly decreases the number of escapeways.

Soil

Soil moisture. – We found that increased soil moisture was significantly related to increased woodcock foraging activity. Glasgow (1958) listed high soil moisture as a factor common to nearly all types of feeding sites. Ensminger (1954) noted the importance of soil moisture in the distribution, abundance, and activity of

Table 2. *One-way analysis of variance of total probe holes in the four soil types.*

Source	Sum of squares	Degrees of freedom	Mean square	F ratio
Between groups	114.781	3	38.260	3.28[a]
Within groups	7,515.881	644	11.671	
Total	7,630.662	647		

[a] Significant at the 0.05 level.

earthworms. Adequate moisture is necessary for earthworms to remain active near the surface (Glasgow 1958). We believe increased soil moisture also permitted probing in areas not generally used by woodcock. On one plot, 4 weeks passed with no probing on or near the plot, but 3 days after heavy rains, when it was partially inundated, more than 1,100 probe holes were recorded within its boundaries. Increased moisture allowed woodcock to probe around obstructions, such as gravel or matted vegetation, which were impenetrable during periods of low soil moisture.

Soil pH. – We found that soil pH significantly affected woodcock foraging activity. Ensminger (1954) reported the greatest abundance of earthworms present in soils with the highest pH values. Sheldon (1967) and Britt (1971) suggested that earthworms were not as important a food source in the South as in northern areas. Although diet composition of woodcock wintering in East Texas is unknown, our findings showed that probing increased with increased pH values. The importance of soil moisture and pH, and other soil characteristics as noted by Kroll and Whiting (1977) for woodcock habitats in Texas, is inconsistent with the findings of Wishart and Bider (1976) for habitats in Canada, suggesting that differences exist between preferred northern summer and southern winter feeding habitats.

Ground Cover

Previous studies in other geographical areas have revealed the importance of ground cover in woodcock habitat selection (Glasgow 1958; Wenstrom 1974; Lambert and Barclay 1975; Fenwood 1976; Wishart and Bider 1976). In our study, two of five ground-cover measurements (percent bare soil and percent litter) significantly affected foraging activity (Table 1). Probe-hole occurrence increased as the percent of bare soil increased and percent of litter decreased. Woodcock foraging methods (i.e., probing) probably necessitate this habitat requirement. These findings also support use of woodcock habitat management practices such as burning, mowing, and thinning (Sheldon 1969; Liscinsky 1972).

Differences in Woodcock Use of Various Soil Types

We found significant differences in the numbers of probe holes in the different soil types (Table 2). Duncan's multiple-range test values grouped numbers of probe holes into two subsets with significantly more probe holes in soils of the Tenaha (47.48) and Bowie (39.81) types than in the Lilbert (13.26) type; the Kirvin (24.29) soil was common to both groups. We also found significant differences in foliage density and soil pH of the different soils (Table 3).

Vegetation

Except for the stratum at 0.00–0.25 m, average FDI's of all strata were significantly higher in the Lilbert soil than in the other three soil types. These groupings are almost exactly the same as those based on the numbers of probe holes by soil type (Table 1). This finding shows the critical importance of foliage density to woodcock foraging in young pine plantations. Although in the Lilbert soil the lowest foliage stratum was not significantly more dense than that of the other soils, increased density in the upper strata possibly reduced the numbers of escape routes and thereby reduced foraging by the birds. These data and our multivariate regression results, whereby increased foliage density in the stratum at 0.26–0.75 m was positively related to increased numbers of probe holes, support Rabe's (1977) conclusion that there is a curvilinear relation between foliage density and woodcock foraging.

Soil

It is noteworthy that none of the ground cover categories nor soil moisture of the soils differed significantly. Soil pH, however, did differ significantly, and the soils were grouped by type, with the Lilbert and Tenaha loamy fine sands in one subset and the Bowie and Kirvin fine sandy loams in another. These results showed that some

Table 3. *Test values for one-way analysis of variance and Duncan's multiple-range groupings of soil characteristics of the four soil types.*

Comparison					Comparison value	Significance value
Percent sand					4.27	0.0002
Soil type	Tenaha	Lilbert	Bowie	Kirvin		
Group means	76.43	74.53	71.04	67.70		
Communality	———	———				
		———	———			
			———	———		
Percent silt					4.22	0.0003
Soil type	Kirvin	Bowie	Lilbert	Tenaha		
Group means	29.56	26.39	23.72	20.67		
Communality	———	———				
		———	———			
			———	———		
Percent clay					0.54	0.0001
Soil type	Tenaha	Kirvin	Bowie	Lilbert		
Group means	3.01	2.74	2.57	1.80		
Communality	———	———	———			
				———		
Percent gravel					3.87	>0.0001
Soil type	Kirvin	Lilbert	Bowie	Tenaha		
Group means	15.49	6.78	4.52	1.48		
Communality	———	———	———			
			———	———		

habitat and soil characteristics varied widely within a soil type.

Although Ensminger (1954) and Miller (1957) found no differences in earthworm numbers in the soils of woodcock and non-woodcock habitats, Ensminger (1954) noted that probing activity increased in more sandy soils. Kroll and Whiting (1977) noted that the percent of sand in the soil influenced diurnal distribution of woodcock. In our study, there was no significant difference in the percent of sand in the heavily used Tenaha soil and in the lightly used Lilbert soil (Table 3). This finding indicates that the percent of sand is an important restricting factor influencing woodcock probing only if it exceeds certain limits. We were unable to define these limits from our data.

Our data indicate that percentages of clay and gravel were more important than sand or silt in affecting woodcock foraging (Table 3). Clay was important because higher clay content increased the moisture-holding capacity of the soil. Increased gravel content probably acted as a physical barrier to probing, especially during periods of low soil moisture. The high gravel content of the Kirvin soil was because 4 of the 18 randomly located plots on that soil type were in areas where the top soil had been scalped off during site preparation. In retrospect, we believe we should have systematically located all plots so that each plot was in an area characteristic of the soil type.

Conclusions

We found woodcock foraging associated with deep, moderately to well-drained soils, typical of upland sites. These soils are quite different from the alluvial bottomland soils generally associated with woodcock throughout the winter range. Soil factors that affected feeding-site selection included soil moisture and pH; both were positively related to numbers of probe holes. Other habitat factors positively associated with probing included the percent of exposed soil and the foliage density of the stratum at 0.26–0.75 m. Factors negatively related to foraging included percent of litter cover and the foliage density of the stratum at 0.00–0.25 m.

We noted significant differences in numbers of probe holes in the different soil types. The preferred soils had relatively low gravel and high clay content. Foliage density of all strata above 0.25 m was higher on the lightly used Lilbert soil type than on the other three more heavily used soils.

Our results suggest several forest management practices that could be used to improve wintering woodcock habitat in southern pine plantations. In upland areas, management efforts should be concentrated on sandy soils with high clay and low gravel content. Site preparation methods in which the area to be planted is sheared and debris is raked into long windrows provide better habitat than those in which the sheared debris is chopped. Hardwood shrubs that grow in the windrows provide overstory cover early in the rotation. Later, after the pines have grown taller than the shrubs, windrows provide escape routes. Escape routes within the pines will exist until later in the rotation if pine seedlings are planted close together in widely spaced rows. Prescribed burning of plantations should be performed as soon as possible in the rotation. Cool winter burns will reduce ground cover without changing mid-story foliage density. Finally, to maintain escape routes and prevent foliage from becoming too dense, stands should be thinned as early and as often as economically possible. These management practices, if used on the proper soils, should allow woodcock to forage in southern pine plantations through most of the rotation.

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Aspects of the History of European Woodcock (*Scolopax Rusticola*) Populations

by

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Abstract

Few historical data on woodcock (*Scolopax rusticola*) populations in some European countries show an extension of the breeding range to the west, corresponding with a population decline in the east during the last century. There is evidence of a population movement from west to east beginning about 50 years ago. The hypotheses that have been proposed, such as variations in hunting pressure or alteration of habitat, do not explain this phenomenon satisfactorily. Some indications suggest that more attention should be paid to climatic changes as a possibly major factor for such large-scale changes in population distributions.

Because the woodcock (*Scolopax rusticola*) dwells diurnally in dense forest cover and is active primarily at night, its distribution is difficult to quantify by direct observation. The presence of courting males is presumed to indicate a breeding population. Although the hunting take may give some indication of woodcock density, the development of woodcock populations has been documented over long periods in only a few European countries. The most recent breeding range and winter quarters of the European woodcock are shown in Fig. 1.

Range Expansion

Great Britain and Ireland

The British Isles have probably always played an important role as winter quarters for woodcock. According to Alexander's (1945, 1946, 1947) investigations, however, there were very few early breeding records. During the 17th and 18th centuries, 27 records were reported from England, none from Scotland, and only one from Ireland. Since 1830 the number of woodcock remaining and breeding in the Isles increased markedly, and by 1900, breeding woodcock were found in nearly all countries of Great Britain and Ireland. Until the 1930's the range expansion continued, with a western tendency, and even small islands were occupied (Shorten 1974). During the last few decades, the populations remained more or less stable, except for local fluctuations that were caused mainly by changing habitat. The distribution maps of 1940 (Alexander 1945) and of 1968–72 (British Trust for Ornithology, Shorten 1974) show similar patterns.

The Netherlands

At the beginning of the 20th century, woodcock bred only occasionally in the Netherlands, but breeding there has increased considerably in the last few decades. In 1961, 203 reports of courting males, nests, and chicks were recorded (Kuiper and Mörzer-Bruijns 1962). Corresponding figures for 1962 and 1970 were 335 (Kuiper 1963) and 400, respectively, and the population growth has continued at least locally into the 1970's (Mörzer-Bruijns, personal communication).

Denmark

According to Clausager's (1972*b*) investigations, although a common migrant, woodcock

Fig. 1. Breeding range (dotted area) and winter quarters (between solid line) of European woodcock (from Kalchreuter 1979a).

have rarely bred in Denmark. During this century, especially in the last few decades, breeding records have increased considerably. The first inquiry of Jespersen (1942) in 1940 revealed 100–200 breeding birds concentrated at four localities. The population then expanded: 750–1,100 breeding females were estimated in 1970; 850–1,250 in 1972; and during the 1970's, the number might well have exceeded 1,500 (Clausager, personal communication).

Other European Countries

No detailed investigations are available for other European countries. Impressions of hunters and foresters, however, point to an increase in the northern parts of West Germany and Belgium (Lippens 1977) in recent years.

There are no historical data from eastern and northeastern countries of Europe, the main production areas of woodcock. However, kill statistics, though gathered only sporadically, represent roughly the abundance of migrating and wintering woodcock and allow some conclusions about the breeding populations in Eastern Europe.

Hoffmann (1867) documented a decline of woodcock in the bag from the 18th to the 19th centuries; since about 1840, there are no longer records of enormous numbers killed on islands along the German Northsea coast, as in some years in the past. However, in recent years (in spring 1965 and fall 1970 and 1977), masses of migrating woodcock were recorded and shot on Heligoland. The hunting bag has also increased in northern Germany in the 1960's and 1970's (Kalchreuter 1979*a*), which might have been caused in part by the increase of the breeding population in Finland since the 1950's (Merikallio 1958; Järvinen and Väisänen 1978).

Discussion of Possible Causes

The coincidence of the decrease of the Eastern European populations with a gradual rise on the British Isles during the 1830's and 1840's strongly suggests a geographical fluctuation from east to west. The reverse tendency about 100 years later is not only demonstrated by the previously described increase of breeding populations on the adjacent continent, but also by banding recoveries. Five birds, banded on the British Isles, were recovered in spring and summer far to the east: two were recovered in Sweden, two in Norway, and one in Russia near Moscow. The bird near Moscow was recovered 2,500 km east of the place of hatching (Kalchreuter 1974). Clausager (1974) mentions three more recoveries as much as 500 km east of the banding origins in Belgium, the Netherlands, and northwest Germany. This pioneering behavior is in contrast to the high homing rates (to the place of hatching) documented by most other recoveries (Kalchreuter 1974) and may thus indicate a mechanism of population increase in the east.

Impact of Hunting

When populations of game birds decline, hunting is commonly believed to be a primary cause. Thus in 1806, when numbers of migrating woodcock declined, the ancient German game biologist Diezel (Hoffmann 1867) expected the woodcock to be extinct within a few decades "because of the incredible persecution." His opinion was then widely accepted and is even today, in spite of the recent breeding population increase. Evaluation of recoveries of birds banded during the 1970's revealed, however, that in the populations that were examined, rates of harvest are considerably lower than rates of overall mortality (Kalchreuter 1979*a*, 1979*b*). Thus, in spite of the increasing number of hunters and despite the annual shooting of about 2 million woodcock in Europe, hunting may not have seriously affected woodcock populations in the past and other factors must contribute to the observed population fluctuations. Despite hunting pressures, new breeding populations have built up in Western Europe.

Effects of Changing Habitat

Woodcock population increase along the Dutch coast has mainly been attributed to changes in habitat coinciding with afforestation programs (Mörzer-Bruijns, personal communication) and reafforestation with deciduous trees after windfall of pure spruce forest. Although such terrain modifications have provided seasonal habitats in Denmark (Clausager 1972*a*), local habitat changes cannot fully explain the widespread and continuous development of these populations. Moreover, the British population in most areas has increased much more rapidly than the habitat has changed. Alexander (1946) described the increase from the first woodcock nest record in a county to its recognition as a "common bird" in only 10 years as a "classic example" for the expansion of woodcock over the British Isles.

Effects of Climatic Changes

Although climatic changes should also be taken into account, reliable climatic data from the last century are not available. Nevertheless, Clausager's (1972*a*) statements about the recent changes of the Danish climate are quite informative: the average precipitation was 10% lower in April, May, and June and 20% higher in July during the period from 1931 to 1960 than in the preceding 30 years. At the same time, the average temperature was 0.5 Celsius degrees higher from April to July and 1 Celsius degree higher in August. The establishment of the Danish woodcock population falls into this period.

The reproductive rate might have been especially affected by such climatic changes because of reduced chick mortality in more favorable weather during the hatching period, and because of improved food conditions during the warm and moist summer weather.

Clark's (1974) evaluation of the wing survey from 1962 to 1976 of American woodcock (*Philohela minor*) revealed the lowest number of young per female in the years when May temperature was above average and the smallest number in the years when May temperature was below average.

Climatic data similar to those for Denmark are not available for the British Isles during the time the woodcock population was expanding. However, the relatively low mortality rates, calculated from recent recoveries, compared with the reproductive potential of woodcock suggest a positive population balance (Kalchreuter 1979*a*). These factors may explain the rapid expansion over the British Isles. After the carrying capacity of the habitat was reached, the population may have expanded to the continent.

The findings summarized here should encourage researchers to pay more attention to climatic influences on woodcock populations.

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Value of Biometric Data in the Determination of Age and Sex in the Woodcock (*S[illegible]pax rusticola*)

by

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Abstract

About 800 woodcock (*Scolopax rusticola*), taken during late winter in Ireland, were examined and age, sex, weight, and body measurements recorded. Clausager's method, using wear of primary feathers, was found to be satisfactory for determining the age of birds until mid-February, after which increased wear on adult feathers caused some difficulty. There is some evidence that a difference in the structure of the barbules of immature feathers may be responsible for the difference in the pattern of wear. Females were heavier than males, but there was a complete overlap of ranges and a tendency for weight to increase during the season. Wing and tail lengths were greater and bill and tarsus lengths less in males, but again there was a complete overlap in ranges. Immature birds were smaller and lighter than adults in all cases. Data were compared with previously published works. There was considerable variation between results, depending on the origin of the sample, condition of the material, time of year, and variations in technique. We infer that such variation renders the use of biometric data less than valuable in assessing the sex of woodcock.

The determination of sex and age, and occasionally the racial structure of a population (or a sample thereof), is of major importance if a wide variety of topics relating to the ecology and dynamics of a species is to be investigated. In an apparently monomorphic species, such determination is usually very difficult without internal examination and is often impossible in the field. The European woodcock (*Scolopax rusticola*) has long resisted all efforts to develop reliable, external characters for age and sex determination.

Intersex and age variations in plumage pattern and color and in the color of the soft parts are usual in birds and can be useful aids to individual identification. Such variation in the woodcock has been considered by several workers (Seebohm 1885; Jackson 1919; Dementiev et al. 1951; Witherby et al. 1940; Orlando 1956; Garavini 1958, 1962; Fadat 1973). Of these findings, many were contradictory and others have been refuted in more recent studies (Fadat 1968; McCabe and Brackbill 1973; Clausager 1973).

In general among the Charadriiformes there is a certain degree of sexual dimorphism in body size, and to a lesser extent, a variation in body size between age groups. There is a general tendency for females to be larger than males, but the reverse is true in many species and biometric characters, either singly or combined in ratios, are used for sexing a wide variety of species (Prater et al. 1977). Little consideration has been given to the seasonal variations that have been demonstrated for most of these characters (Pienkowski and Minton 1973; Prater 1975; Pienkowski 1976; Macgregor and Jones 1979).

Variation in bill length in proportion to body size is often most obvious. Yarrell (1845) claimed that the bill was shorter in juvenile woodcock, whereas Ogilvie-Grant (1912) noted that the female woodcock bill was almost always longer than that of the male. Witherby et al. (1940), Dementiev et al. (1951), Glutz von Blotzheim et al. (1977), and S. Cramp and K.E.L. Simmons (unpublished data) give data for woodcock of known age and sex. In recent years the emphasis has been on a search for biometric variation to distinguish between the sexes, such as is available for the American woodcock, *Philohela minor* (Greely 1953; Martin 1964; Artmann and Schroeder 1976).

McCabe and Brackbill (1973) examined a variety of biometric characters as well as plumage and feather variation in 100 woodcock from Ireland during the winter 1968–69 but found little difference between sex or age groups. Clausager (1973) described a method of age determination for juvenile and adult (more than 1 year old) woodcock based on primary wear, the pattern on the primary coverts, and the pattern on the underside of the tail feathers. The technique based on primary wear is similar to that described by Sheldon et al. (1958) for *Philohela*. In addition, Clausager found significant differences between male and female bill and tail measurements and proposed the use of a ratio of these characters which sexed 42% of adult males, 46% of adult females, 28% of juvenile males, and 20% of juvenile females. Stronach et al. (1974), with a sample of 614 woodcock from Ireland, used a discriminant analysis of the linear function of bill and tail lengths to differentiate between males and females. This technique is claimed to sex 75% of the males and 72% of the females, with a 28% probability of misclassification.

Material

A total of 790 birds collected during the seasons 1975 to 1977 were available for analysis. Most of the birds were taken in February by members of the National Association of Regional Game Councils, under special license from the Forest and Wildlife Service and came from counties Cork, Mayo, and Donegal. Specimens were kept deep frozen until analysis.

Birds were sexed by dissection, and age was determined by the method of Clausager (1973), using the pattern and extent of wear on the primaries. Adult woodcock molt completely between July and October (Dementiev et al. 1951). Primary molt begins in late July and is generally completed by the end of September. Juveniles undergo a partial molt during the same period, but retain all of the primaries and the outer secondaries. Thus, at any time from October onwards, the primaries of juvenile woodcock will be, on average, 2 to 3 months older than those of adults. In addition, however, Clausager (1973) found that, as was the case with *Philohela* in North America (Sheldon et al. 1958), the pattern of wear differed in adult and juvenile primaries, and our findings confirm this. The barbs and barbules of adult feathers appear to be more robust than those of the juvenile, and wear occurs evenly. Consequently, on gross examination, the edge and tip of an adult primary appear entire. In contrast, in the juvenile feathers, barbules snap off the barb at their base and, indeed, entire sections of the barb may break away, giving a frayed or ragged outline to the feather (Fig. 1). The broken barbs are generally visible with the naked eye, but magnification of up to 20 × may be necessary to detect such wear in the early part of the season or to check the identification of adult feathers in the spring. Wear is always more noticeable on primaries 7 to 9.

We considered primary wear to be more reliable for age determination than either of the other methods used by Clausager (1973). Tail feather pattern was considered unreliable because some juvenile woodcock may molt some or all of their tail feathers before February. The color and size of the distal light fringe on the primary coverts was found to be more variable than Clausager suggested, although generally birds with very narrow light fringes showed the adult pattern of primary wear and those with broad fringes had juvenile-type primaries. The pattern of primary covert fringes was useful in some cases where primary wear was indistinct or borderline. None of the birds examined showed any sign of a Bursa of Fabricius.

Birds were weighed to the nearest 2 g and the following measurements taken: wing length (from the carpus to the tip of the longest primary along the flattened, straightened, and unspread wing), tail length (from the coccyx to the tip of the central tail feather along the underside), bill length (from the tip to the cere along the upper

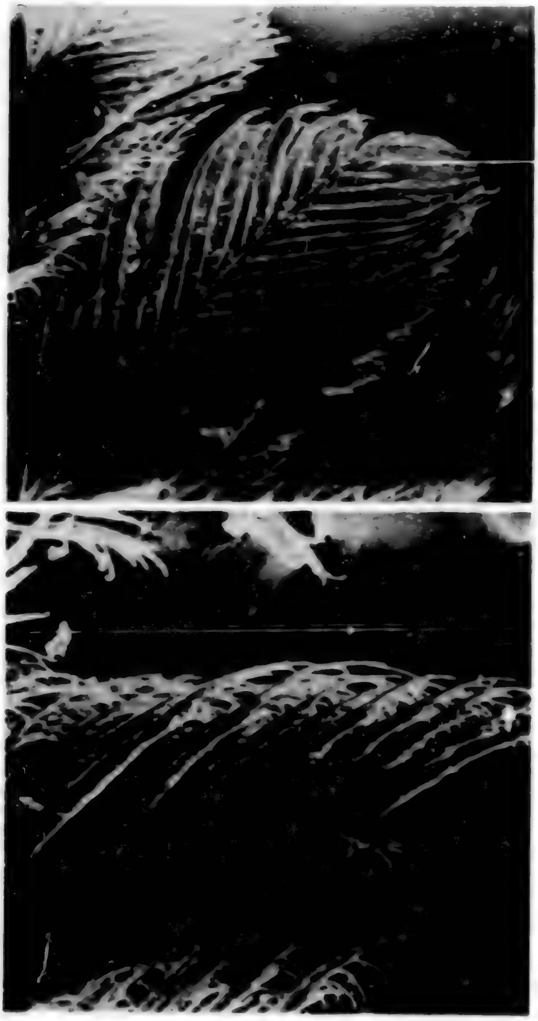

Fig. 1. Scanning electron microscope photographs (× 300) of adult (upper) and immature (lower) primary feathers showing pattern of wear on barbs and barbules.

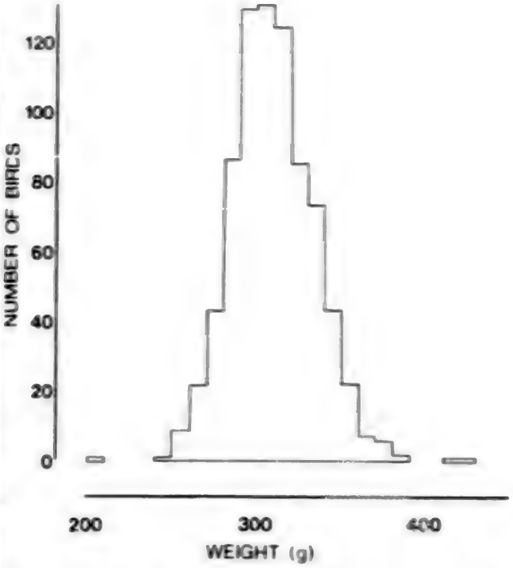

Fig. 2. Weight distribution of 785 *Scolopax rusticola* taken in February.

mandible), and tarsus length (from the back of the intertarsial joint to the front of the middle toe). Means, ranges, standard deviations, and coefficients of variation of all measurements taken are given in Table 1. Also shown are t values to test the significance of difference between birds of different sex.

Weight

Weights of 780 woodcock were extremely variable, with a mean of 307.3 ± 24.4 g for the total sample (Fig. 2). Female mean weight was greater than that for males by 6.1 g (310.6 ± 24.1 to 304.5 ± 24.2 g, $t = 3.548$, $P < 0.001$) and adult mean weight greater than that of immatures by 5.9 g (309.6 ± 26.0 to 303.7 ± 21.1 g, $t = 3.478$, $P < 0.001$), but there was an almost total overlap of ranges with the heaviest birds, an adult male of 410 g and an adult female of 420 g (both on 23 February 1975) and the lightest, an adult female of 205 g (2 February 1975), falling somewhat outside the more normal range of 250 to 390 g.

A slight (insignificant) increase in weight was observed during February, and a small sample (n = 34) of birds taken in the early part of the winter showed a peak in body weight in December–January, falling to a low in early February. Data on monthly mean weights (Fig. 3) of woodcock from this study, from Ireland and Scandinavia, data collected from the British Museum at Tring, and reports by Glutz von Blotzheim et al. (1977), Marcstrom (1974), and Fadat (1969) show a seasonal bimodal pattern similar to those exhibited by many littoral scolopacids (Macgregor and Jones 1979). This pattern is closely linked to the breeding–migration–molt strategy of the species, but similarities can also be observed with the seasonal availability of lumbricids and other prey items on or near the surface (Bouché 1972).

Table 1. *Means, ranges, standard deviations, and coefficients of variation of* Scolopax rusticola *biometrics.*

Measure	Class	No.	Range	Mean	S	C(%)[a]	*t*-test for sex[b]
Wing (mm)	M	404	182–218	201.51	5.46	2.7	6.450***
	F	375	186–213	199.12	4.88	2.5	
Tail (mm)	M	347	71–98	86.21	3.93	4.6	12.851**
	F	331	70–94	82.39	3.81	4.6	
Bill (mm)	M	395	58–92	70.91	3.24	4.6	10.264***
	F	371	46–88	73.50	3.71	5.0	
Tarsus (mm)	M	245	30.5–39	36.20	1.23	3.4	8.211***
	F	245	33.7–40.8	37.12	1.25	3.4	
Weight (g)	M	405	250–410	304.48	24.17	7.9	3.548***
	F	377	205–420	310.61	24.11	7.8	

[a]Coefficient of variation expressed as a percentage.

[b]Significance: *** = $P < 0.001$.

Body Measurements

The four body measurements (lengths of wing, tail, bill, and tarsus) that were regularly taken exhibited far less variation than did weight. Wing length for 782 birds ranged from 182 to 218 mm around a sample mean of 200.4 ± 5.4 mm. Male mean length was greater than that of females by 2.4 mm (201.5 ± 5.5 to 199.1 ± 4.9 mm, $t = 6.450$, $P < 0.001$), and adult mean length was greater than that of immatures by 2.0 mm (201.1 ± 5.23 to 199.1 ± 5.4 mm, $t = 4.998$, $P < 0.001$). Again, there was a total overlap of ranges, with the shortest and longest wings both belonging to adult males (Fig. 4).

Wing length data from other studies show a certain degree of variation, much of which can be attributed to variations in the condition of the material (Green 1980; Knox 1980) and to variations in operator technique (Evans 1964; Spencer 1976). However, the possibility that seasonal or regional variations (or both) exist cannot be excluded. To exclude the effect of variation in operator technique, wing lengths of 127 woodcock in the British Museum at Tring were measured by the senior author. These birds were drawn from four main areas covering almost half the entire world range of the species (Fig. 5). There was no significant difference between the means for the four areas ($F = 0.10107$, $P > 0.05$), suggesting that operator technique is perhaps the greatest variable in wing length data.

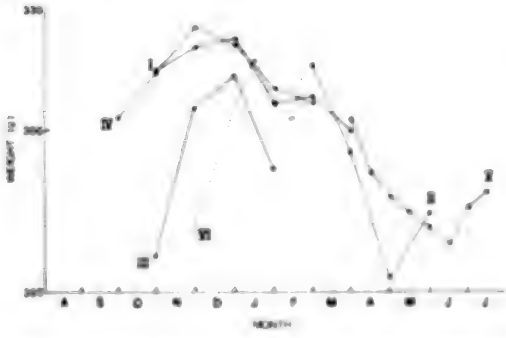

Fig. 3. Seasonal fluctuations of mean body weight of *Scolopax rusticola*. Sources: I Ireland (Present study), II Scandinavia (Present study), III British Isles – British Museum collection, IV France – Glutz von Blotzheim (1977), V Sweden – Marcstrom (1974), VI France – derived from Fadat (1969).

Mean wing length for the 68 birds from the British Isles in the collection was 193.9 ± 7.5 mm. Compared with the mean of the fresh specimens of 200.4 ± 5.4 mm, this finding suggests a postmortem shrinkage of 3%, which is in line with that reported by Prater et al. (1977), Green (1980), and Knox (1980).

Tail lengths ranged from 70 to 98 mm about a sample mean of 84.3 ± 4.3 mm. Ranges for males and females overlapped almost completely, but their distributions showed an opposite skew (Fig. 4) that was quite marked, especially among adult birds. Mean male tail length exceeded that of females by 3.8 mm (86.2 ± 3.9 to 82.4 ± 3.8 mm, $t = 12.851$, $P < 0.001$), and adult mean tail length exceeded that of immatures by 2.2 mm (85.2 ± 4.2 to 83.0 ± 4.2 mm, $t = 6.644$, $P < 0.001$). As with remiges, it is considered that each molt produces retrices of increased length. Since some but not all immature woodcock molt their tail

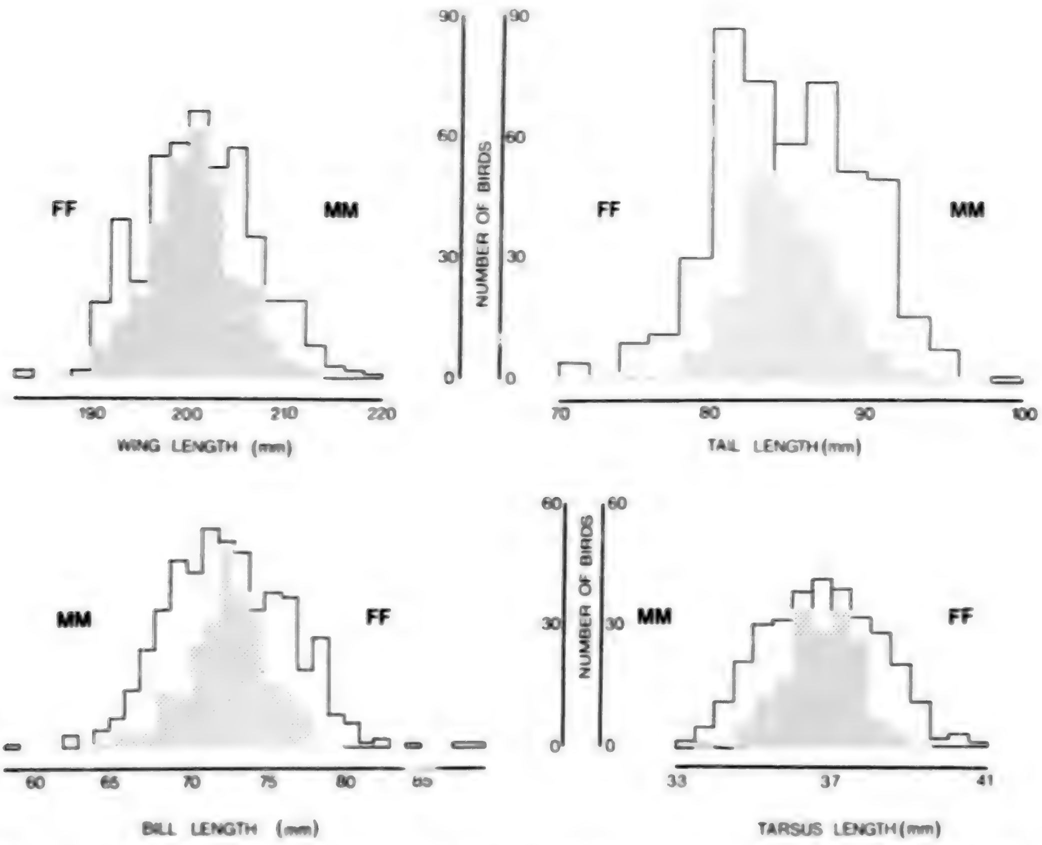

Fig. 4. Sex variation in biometrics of *Scolopax rusticola* taken in Ireland. Stippled areas show overlap of distributions. (FF = females, MM = males.)

feathers in the autumn (Clausager 1973), tail feathers of two different ages exist in the immature sample, leading to an extension of the range on the positive side.

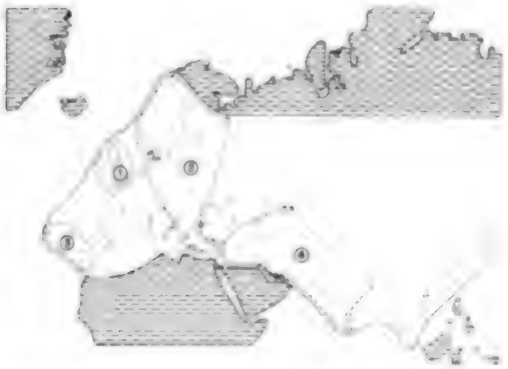

Fig. 5. Map showing range of *Scolopax rusticola* and the four sample areas for which biometric comparisons were made.

Bill length (from tip of upper mandible to cere) for 769 woodcock ranged from 42 to 96 mm. However, the birds with bills of 42 mm (an adult female) and 96 mm (an adult male) were exceptional, and at least the female was almost certainly deformed (Fraguglione 1979). The range for the remaining 767 birds was from 58 to 88 mm around a sample mean of 72.2 ± 3.7 mm. Excluding the two birds mentioned above, there was a small amount of non-overlap in the ranges (2%), with males from 58 to 80 mm and females from 64 to 88 mm. Female mean bill length exceeded that of males by 2.6 mm (73.5 ± 3.7 to 70.9 ± 3.2 mm, $t = 10.264$, $P < 0.001$), but there was no significant difference between the means for adults and immatures (72.2 ± 4.0 and 72.2 ± 3.3 mm, respectively, $t = 0.076$, $P > 0.9$). Variation in bill length has long been used as an aid in sex determination of Charadriiformes, but in recent studies dissatisfaction has been expressed as to the consistency of the conventional tip-to-cere measure. Pienkowski (1976) showed a seasonal variation in bill length of knot (*Calidris canutus*) in eastern England that can be attributed to seasonal change at the feather-cere margin at the base of the upper mandible associated with abrasion and molt or with a seasonal change in the growth or wear (or perhaps degree of compression) of the rhamphotheca related to feeding conditions. Change in the rhamphotheca has been suggested for passerines by Stettenheim (1972) and could occur in oystercatcher, *Haematopus oestralagus* (White and Gittens 1974) and turnstone, *Arenaria interpres* (Summers 1976), where the rhamphotheca extends well beyond the bone.

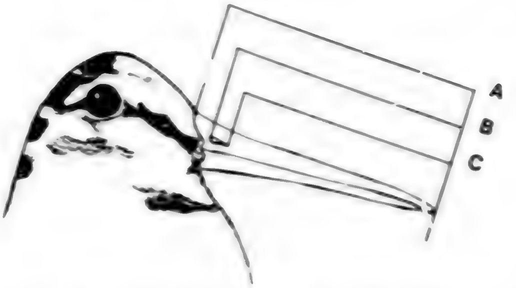

Fig. 6. Methods used in measuring the bill of *Scolopax*: A. bill tip to cere (conventional); B. bill tip to rear of nostril; C. bill tip to front of nostril (nalospi).

X-ray analysis shows that the rhamphotheca on the upper jaw of the woodcock extends up to 2 mm beyond the premaxilla and thus forms a well-developed notch into which the lower jaw fits (Burton 1974). The tip is relatively hard (in comparison with that of the snipe, *Gallinago gallinago*) and contains the numerous Herbst corpuscles used in the location of prey (Stettenheim 1972; Schwartzkopff 1973; N. Stronach, personal communication). No evidence exists to show that variations in this area occur in live Charadriiformes, and it is safe to suppose that if any such variations did occur they would be insignificant in terms of overall bill length in a long-billed species such as the woodcock. Variation in the position of the feather-cere margin is far more likely, but again data to test this hypothesis do not exist for the woodcock. To eliminate any such variation, Pienkowski (1976) suggested a measure taken to the rear of the nostril, and many continental workers favor a measure taken to the front of the nostril (nalospi) (Fig. 6). Some 240 birds were measured by members of staff of the Forest and Wildlife Service, using both the conventional method and one or other of these measures. Both measures were well correlated with the conventional measure ($r = 0.94$ and 0.92 respectively, $P < 0.001$), differing by 4.5 and 10.3 mm, respectively. Bill length was measured for 118 specimens in the British Museum at Tring. The mean value (71.9 ± 3.9 mm) showed no significant decrease (0.43%) from the mean for the fresh specimens (72.2 ± 3.7 mm, $t = 0.8149$, $P > 0.4$). Summers (1976) showed that turnstone bills with the rhamphotheca extending well beyond the bone may shrink by up to 5.4% whereas sanderling (*Calidris alba*), with a closely fitting rhamphotheca, showed only 2.7% shrinkage. Greenwood (1979), however, found no significant decrease in bill length of dunlin (*Calidris alpina*). Any decrease in woodcock bill length due to shrinkage of the rhamphotheca may be masked by shrinkage and retraction of the cere margin, causing a similar increase in apparent length. No significant differences were found in the bill lengths of birds from the four regions (Fig. 5).

Mean tarsus length for 490 birds was 36.66 ± 1.32 mm (range, 30.5–40.8 mm). There was a small amount of non-overlap between the sexes (accounting for 1.5% of the sample), with males ranging from 30.5 to 39.0 mm and females from 33.7 to 40.8 mm. Mean tarsus length of males was shorter than that of females by only 0.92 mm (36.20 ± 1.23 to 37.12 ± 1.22 mm), but this difference was highly significant ($t = 8.211$, $P < 0.001$). There was no significant difference between tarsus lengths of adult and immature birds (36.67 ± 1.30 and 36.66 ± 1.36 mm, respectively; $t = 0.126$, $P > 0.9$).

Since the mean bill and tarsus lengths of immature and adult woodcock are similar, it would appear safe to assume that young woodcock are fully grown with respect to body size by their first winter (in agreement with Fadat 1974), although they are still lighter than adults and their immature feathers are shorter. Samples of measurements (where available) taken in February for each age and sex class in each of three years were compared. Differences between yearly means are very slight and significant in only 2 of 12 cases. It has been suggested that immature mallard (*Anas platyrhynchos*) reared in unfavorable seasons may have smaller bones, leading to annual variations in immature bone measurements (Owen and Montgomery 1978).

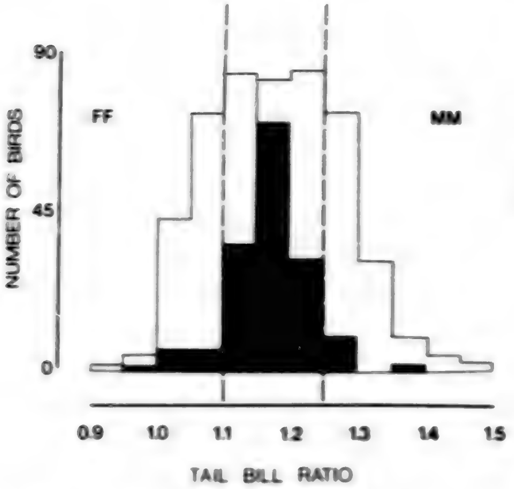

Fig. 7. Distribution of tail : bill ratio in *Scolopax rusticola*

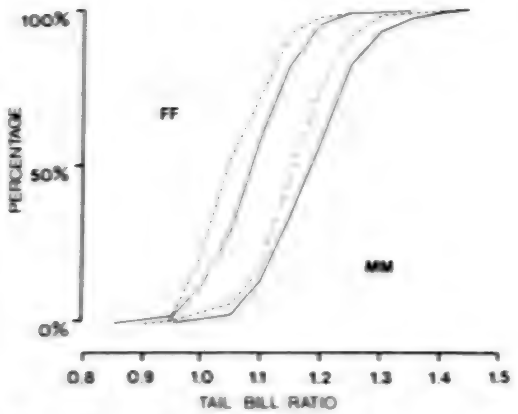

Fig. 8. Cumulative distribution of *Scolopax rusticola* tail : bill ratio (solid lines – adult birds, broken lines – immature birds).

but this does not appear to apply to woodcock. The number of years available did not allow detailed comparisons to be made, and little significance should be attached to these results.

Ratios

Many workers have criticized the use of ratios as indices for characterizing samples because they are usually correlated with size and thus misleading for comparison of samples (Northcote 1979). Ratios in general use contain only two characters and thus afford a poor appreciation of what may be an involved contrast between forms. To compound two characters into a ratio implies that there is only one contrast of form to be studied and that the unique contrast is well assessed in terms of two characters of equal weight but opposite sign, which is almost invariably not the case (Blackith and Rayment 1971).

Notwithstanding, ratios have frequently been employed to differentiate between groups of birds (i.e., sex classes, regional groups). For characterizing the sexes of woodcock, a simple ratio of tail length:bill length is probably best because these two measures are independently variable and show the greatest intersex variation and, particularly in respect to bill length, the least variation with age. Mayr et al. (1953) and Simpson et al. (1960) recommended that comparisons of ratios should be obtained as smaller:larger ratio rather than vice versa. However, as variability is usually greater for the larger value, the reverse is often more convenient. A drawback of ratios is that *t*-tests on comparisons of ratios can produce different levels of significance, depending on the form of the ratio (Northcote 1979).

Tail:bill ratios were calculated for 659 birds and their distribution is shown in Fig. 7. The tail:bill ratio for 336 males was on average 1.218±0.075 (range 0.95–1.45), and for 321 females the average value was 1.124±0.077 (range 0.90–1.70). However, the single female with a ratio of 1.70 was the bird previously mentioned with a 46-mm bill that was probably deformed. Ignoring this value, males ranged from 0.95 to 1.45 and females from 0.90 to 1.35, still an almost total overlap of ranges, with only 1.7% of the sample falling in the zone of nonoverlap. From the cumulative tail:bill data (Fig. 8) for each of the four age–sex classes, it can be seen that there is an 80% probability of birds with ratio values of 1.20 or higher being males and birds with ratio values of 1.15 or lower being females. However, 23.5% of the population lies in between. Only 1.7% of the birds can be sexed with 100% certainty, unlike the 42–43% found by Clausager (1973), who used a smaller and more homogenous sample.

As previously mentioned, bills of immature woodcock are already fully grown by the first winter, whereas their tail length is on average shorter than that of adult birds. Consequently, the tail:bill ratios for immature birds were less than for adults. The average value for 134 immature males was 1.20±0.07 and for 118 immature females was 1.10±0.07 (compared with 1.23±

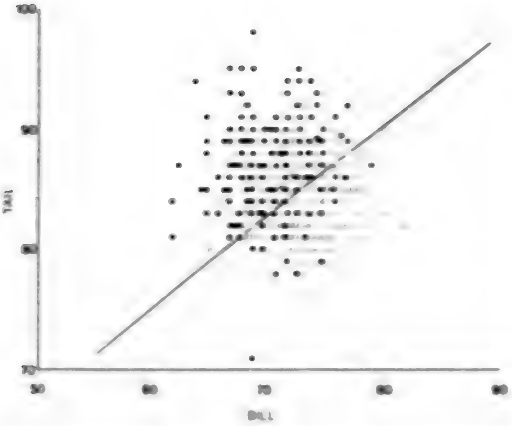

Fig. 9. Scatter of points indicating male • and female

0.08 and 1.14 ± 0.08 for 201 adult males and 203 adult females, respectively). Non-overlap was 0.79% among immatures and 2.2% among adults.

Devort (1977) favored the use of a tail length × wing length:bill length ratio (the indice de sexualite [Is] of Fadat 1977). Given that there is a high degree of correlation between wing and tail lengths, coupled with the inconsistency (seasonal and interoperator variation) involved in taking wing measurements, we did not consider this method suitable for the present study.

Discriminant Analysis

The multivariate technique of discriminant analyis considers variates collectively. A calculation is made of the linear function of the variates that results in the maximum separation of the required groups. Statistical methods to derive discriminant functions are described by Blackith and Rayment (1971). The method of Dixon (1973) was followed in the present analysis.

Some measurements are clearly more sensitive to "sexual difference" than others. Bill and tail lengths are regarded as the most dependable of the five standard measures because they exhibit the least seasonal variation. They were combined with each other and with wing and tarsus lengths to give the following discriminant functions:

D-1 0.00071 tail − 0.00054 bill = 0.02089

D-2 0.00064 tail − 0.00057 bill + 0.00012 wing = 0.03683

D-3 0.00072 tail − 0.00051 bill − 0.00027 tarsus = 0.01373

The scatter of points indicating male and female measurements related to D-1 above (males above the line, females below) is shown in Fig. 9. Some points lie on the discriminant line, while many others, both males and females, lie on the wrong side of the line. Normal curves for the data show that for a combination of tail and bill, 24.4% of males and 23.9% of females would be wrongly sexed (overall, 24.1%). The percentages wrongly sexed by combinations of tail, bill, and wing and of tail, bill, and tarsus were higher at 25.1 and 24.4%, respectively.

Discriminant functions were also calculated for the following combinations:

D-4 0.00063 tail − 0.00054 bill + 0.00015 wing − 0.00034 tarsus = 0.03185.

D-5 0.00066 tail − 0.00050 bill + 0.00018 wing − 0.00029 tarsus − 0.00004 weight = 0.03323.

D-6 0.00067 tail − 0.00052 bill + 0.00016 wing − 0.00004 weight = 0.03736.

D-7 0.00058 tail + 0.00009 wing − 0.00006 weight = 0.05769.

D-8 0.00031 wing − 0.00005 weight = 0.0483

Charactres are weighted in a manner that maximizes the separation between the sexes in the order tail, bill, tarsus, wing, and weight.

All eight discriminant functions give similar probabilities of misclassification on the order of 23 to 38%, on the basis that the two most variable characters alone would give a maximum of 38.2%. The best classifications were given by D-4 and D-5, with 22.9 and 23.4% probability of misclassification, respectively; in view of the enormous seasonal variation in weight and possible operator variation in wing measurement, however, these are of little use in ongong interoperator studies. We believe that D-1 and D-3 are therefore the most useful discriminant functions for use in such work, and this conclusion is in general agreement with the findings of Stronach et al. (1974), who reported a 28% probability of misclassification when using a similar function of tail and bill lengths.

Conclusions

It can be seen that despite the significant sexual differences in body size and shape, there is a very great deal of intersex variation in the woodcock. By using any or all of the biometric characters that were investigated, only a very small percent of woodcock can be sexed with absolute certainty; for the majority there is at least a 25% probability of the incorrect sex being assigned. Clearly this is not satisfactory, and the search for a distinctive secondary sexual character must continue.

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Movements, Home Ranges, and Habitat Use of Wintering Woodcock in Ireland

by

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Abstract

Twelve radio-marked woodcock (*Scolopax rusticola*) were studied from 14 November 1979 to 16 April 1980 near Rathdrum, County Wicklow. The radio-marked woodcock, six adults and six immatures, were monitored for a total of 708 transmitter days (range 12 to 124 days). Distances moved and flight times in relation to cloud cover at dawn and dusk were recorded. Movements at dawn and dusk were regular between diurnal and nocturnal locations. The preferred diurnal habitat type was young planted coniferous woodland (thicket stage), whereas pasture fields were selected at night. At night, in cultivated fields (predominantly winter barley), woodcock selected unploughed margins and the small marshy areas situated in some of these fields. The composite home-range area for 11 radio-marked woodcock (excluding one bird located 4.15 km outside the study area) was 251 ha, with individual composite home-range sizes varying from 14.9 to 74.4 ha. The recurrence of woodcock at the same wintering sites in successive seasons is discussed in relation to the findings of this study.

The woodcock (*Scolopax rusticola*) is, by tradition, hunted in Ireland. Management of this species or its habitat during winter has been carried out without any real knowledge of the bird's actual behavior. Until recently, information on the behavior of woodcock in winter has been largely anecdotal.

By using retrap data obtained from a woodcock ringing program in Ireland (1974–75 to 1978–79), Wilson (1980) showed that wintering woodcock were faithful to areas of daytime cover (< 300 ha in size) for short periods (20 days) within a winter period and returned to the same areas of daytime cover in successive winters. He also suggested that the absence of any pattern in the occurrence of recaptures in subsequent winters indicated that woodcock were sedentary within any winter period. A subsequent radiotelemetry program in Ireland and one in England during winter 1978–79 (Wilson 1980; Hirons 1980; G. Hirons, personal communication) confirmed fidelity not only to areas of daytime cover but also to groups of fields at night in the short term (6 weeks), even under adverse weather conditions. Local movement (within 10 km of the study area) was recognized as a consistent, though minor, element of winter behavior.

The present paper presents information on the diurnal and nocturnal movements, habitat preferences, and degree of fidelity shown to areas of daytime cover and nighttime fields by individual radio-marked woodcock during one winter.

Study Area Location and Habitat Types

The study area was located 3 km north of Rathdrum, County Wicklow. The area lies on the eastern edge of the Wicklow mountains at an altitude between 115 and 285 m above mean sea level. The topography is rolling. The soils are acid brown earths and associated brown podzolics derived from mica-shist glacial till and underlying Ordovician shale (Gardiner and Ryan 1969).

An arbitrary boundary encompassing the composite home range of the radio-marked woodcock defines the study area (Fig. 1). The total study area is 490 ha, of which 247 ha are planted coniferous woodland, including a small stand of semi-natural oak (*Quercus petraea*) woodland. The remainder is agricultural land, of which 72.5 ha are pasture and 170.5 ha are cultivated. Six major habitat types are recognized and described, together with the percentage occurrence of each habitat type on the 490-ha study area.

Coniferous plantation (18.8%).—Planted coniferous woodland, 13 to 23 years old or thicket stage, averaging 8 m high and consisting of the following species, established mostly in pure blocks: Sitka spruce (*Picea sitchensis*), Norway spruce (*Picea abies*), Douglas fir (*Pseudotsuga menziesii*), Scots pine (*Pinus sylvestris*), Corsican pine (*Pinus nigra* var. *maritima*), and Japanese larch (*Larix leptolepis*). Ground vegetation is generally sparse or absent, especially beneath the tightly closed canopy of spruces and fir. On the fringes of the woodland blocks, along roads and ride-lines (unplanted strips 6–8 m wide within the woodland area), and in openings within the woodland, grasses occur with occasional patches of bracken (*Pteridium aquilinum*), bramble (*Rubus* spp.), and gorse (*Ulex gallii*).

Coniferous plantation (24.5%).—An area predominantly occupied by semimature or pole-stage Scots pine (averaging 18 m) planted between 1926 and 1947 and managed for timber production. It has well-developed ground vegetation consisting of grasses, bramble, bilberry (*Vaccinium myrtilus*), and woodrush (*Luzula sylvatica*).

Oak (0.8%).—A small area of semi-natural sessile oak woodland with an understory of birch (*Betula pubescens*) and willow (*Salix* spp.). Woodrush and bilberry predominate in the ground vegetation.

Clearcut (6.2%).—A clear-felled area within the main woodland block, replanted recently (2–3 years ago) with Douglas fir, Japanese larch, and Noble fir (*Abies nobilis*) that have not yet attained an average height of 1 m. There is natural regeneration of birch, mountain ash (*Aucuparia aucuparia*), and holly (*Ilex aequifolium*), although the area is heavily browsed by deer. The ground vegetation is dominated by grasses, bilberry, and woodrush, with bramble and heather (*Calluna vulgaris*) locally abundant.

Fig. 1. Map of the study area, showing the habitat types and the composite home range boundary for 11 radio-marked woodcock.

Pasture (14.9%).—Fields of permanent, fertilized grassland grazed by sheep and cattle until late autumn (November). Field sizes vary from 2.3 to 7.3 ha (average, 4.5 ha). All fields are surrounded with stone and earth banks that support a variety of tree species, including oak, ash (*Fraxinus excelsior*), and sycamore (*Acer pseudoplantanus*); shrub species, namely holly, gorse, hawthorn (*Crataegus monogyna*), and willow; and a ground vegetation that includes grasses, bracken, and bramble.

Cultivated land (34.8%).—Winter barley (*Hordeum* spp.), sown in October, occurred on

80% of this area (170.5 ha); the remainder was ploughed in preparation for spring sowing of cereals. Field sizes varied from 1.3 to 67.2 ha (average, 10.9 ha). Winter barley formed a loose sward 3–5 cm high on the fields for the period of the study. Unploughed margins (about 1 m wide) occurred around the periphery of each field and supported a grass sward. Certain of the winter barley fields contained wet marshy areas ranging from 0.2 to 1.8 ha (see Fig. 1). These areas were characterized by a high water table, by being unploughed, and by supporting a variety of grass species, rushes (*Juncus* spp.), and willow on parts close to field boundaries.

Methods

Radiotelemetry Procedures

A total of 12 woodcock at the study area were equipped with transmitters between November 1979 and January 1980. The woodcock were caught in mist nets placed across forest roads and set for birds arriving at dawn (Wilson 1980). Each woodcock was weighed, measured, ringed, and aged by the method of Clausager (1973) and then fitted (Wilson 1980) with one of two types of transmitters. Transmitters were powered by mercury or lithium batteries. The lithium-type transmitter was 36% heavier but operated more than twice as long as the mercury-powered type. Both transmitter types were used for this study because the efficiency of the mercury type was greatly reduced by periods of cold weather with frost or snow and although the lithium transmitter overcame this problem, it was heavier and more bulky. It was considered safer to employ the two types of transmitters alternately during the study period, in case the lithium transmitters should prove too heavy or cumbersome for woodcock.

When they were released (close to capture points), the radio-marked birds flew an average of 101 ± 72 m ($\bar{x}$ ± SD), usually along a forest road, before pitching into adjacent cover. Birds that did not acclimate to the radio package on the first evening after radio-marking were flushed the following morning to observe the effects of the transmitter package on flight. This process was maintained until the bird voluntarily flew at dusk from cover, usually 1.4 days after radio-marking (range, 0.4 to 3.4 days).

Radio-marked birds were located on foot by using a portable receiver (Model LA12, AVM Instrument Company) and a three-element hand-held yagi antenna. Maximum transmitter range was about 8.0 km, but tracking and fixing of positions was normally undertaken (using triangulation) at distances less than 200 m on fields at night when the radio-marked birds could be readily placed within a particular field, and was performed at much closer range when a bird's position was uncertain. The presence of a high density of forest roads and ride-lines allowed diurnal positions in cover to be "fixed" at distances generally less than 100 m.

Home Range and Habitat Use Measurements

The position of each bird was determined at dawn and dusk in both its habitats (nocturnal and diurnal) and recorded on habitat maps of the study area (scale, 1:10,560 m). Winter home ranges (i.e., diurnal, nocturnal, and composite) of each radio-marked woodcock were measured, using a planimeter, from the polygon formed by connecting the outermost location points. Occasional locations (sallies) more than 2 km from the study area were ignored in home-range calculations. Within each woodcock's diurnal and nocturnal home ranges, the smallest area encompassed by at least 67% of the location points was designated an activity center (Horton and Causey 1979).

Nocturnal and diurnal locations obtained within the voluntary flight period but excluding nonclassifiable (habitat) locations (about 3%) were plotted on habitat maps. The number of diurnal and nocturnal locations per bird by age class was recorded for each habitat type. Using these data and the areas of each habitat type within the composite home-range boundary (see Fig. 1), a modified habitat preference index (MPI) was calculated (Wenstrom 1973). Habitat preference and intensity of use were tested by Chi-square analysis, and a probability level of 0.05% was used to indicate significance.

Cloud cover and departure times at dawn and dusk were noted for selected radio-marked birds throughout the study period.

Marking Results

Migratory woodcock joined the small resident population of birds on the study area in late

Table 1. *Periods of recording and details for 12 radio-marked woodcock.*

Birds and age	Weight (g)	Transmitter type[c]	Date equipped	End of tracking period	Transmitter[a] days	Data[b] days	Notes
Adult							
A	304	L	22 Nov 1979	6 Mar 1980	47[d]	44	Transmitter failed
B	285	M	22 Nov 1979	9 Dec 1979	18	16	Transmitter failed
C	308	L	28 Nov 1979	29 Mar 1980	124	121	Migrated
D	320	L	30 Nov 1979	14 Dec 1979	15	15	Died, bill caught in harness
E	330	L	20 Dec 1979	4 Apr 1980	107	106	Migrated
F	345	L	14 Jan 1980	16 Apr 1980	93	93	Migrated
Immature							
G	290	M	14 Nov 1979	5 Dec 1979	22	19	Transmitter failed
H	335	M	16 Nov 1979	13 Dec 1979	28	26	Transmitter failed
I	283	M L	23 Nov 1980	17 Mar 1980	116	116	Recaptured, transmitter removed
J	340	L	19 Dec 1979	29 Mar 1980	102	99	Migrated
K	320	L	12 Jan 1980	24 Jan 1980	12	9	Died, broken tip to lower mandible
L	296	M	15 Jan 1980	8 Feb 1980	24	21	Transmitter failed

[a] Transmitter days = the number of days a transmitter functioned.

[b] Data days = the number of days from which locations were used, excluding a period of adjustment following radio-marking.

[c] L = lithium-powered transmitter; M = mercury-powered transmitter.

[d] Bird A was located 4.15 km east of the study area capture point 59 days after radio-marking.

autumn. They arrived in early November 1979 (sudden appearance of flighting woodcock at dawn and dusk) and were present until late March to mid-April 1980. Twelve woodcock (six adults and six immature), fitted with radio transmitters in November and December 1979 and January 1980, were monitored for periods of 12 to 124 days ($\bar{x} = 59$) from 14 November 1979 to 16 April 1980 (Table 1). Ten of the birds were first-time captures and two were recaptures, one from 13 January 1978 and the other a radio-marked bird from the previous winter (30 January 1979) with its radio transmitter still in place.

The 12 birds were successfully radio-tracked for a total of 708 days, yielding 685 data days and 2,229 locations in diurnal and nocturnal habitats. Two birds died within 12 and 15 days of radio-marking, the first from starvation due to a broken tip of the lower mandible (possibly sustained when released) and the second from entangling its bill in the transmitter harness. Four other instances of the bill becoming trapped in the transmitter harness were recorded, three times with Bird I and once with Bird B. In these instances the harness had loosened slightly, and the problem was remedied by tightening the harness or equipping the bird with a new transmitter package.

Birds G and H were recaptured in mist nets 7 and 5 days, respectively, after radio-marking. The weight of Bird G was the same as when it was radio-marked, but Bird H had lost 2% of its body weight; when Bird I was found after 116 days with its bill caught in the transmitter harness, it had lost 3% of its body weight. Slight feather wear (axillary region) was apparent only on Bird I after 116 days.

The radio-marked woodcock adapted quickly to the transmitter packages, which did not appear to influence their normal activities or cause injury even after prolonged use. Birds with the heavier lithium-battery transmitters moved the greatest distances; for instance, Bird A reestablished itself 4.15 km from its capture point and on two occasions used an alternate woodland block 7.9 km away as daytime cover, and four other birds moved to fields at dusk of the day they were radio-marked.

At night, three of the radio-marked birds initially favored the use of a clearcut area adjacent to their daytime cover (1 to 9 nights), which suggested either that the period of acclimatization may be longer for some birds than for others or

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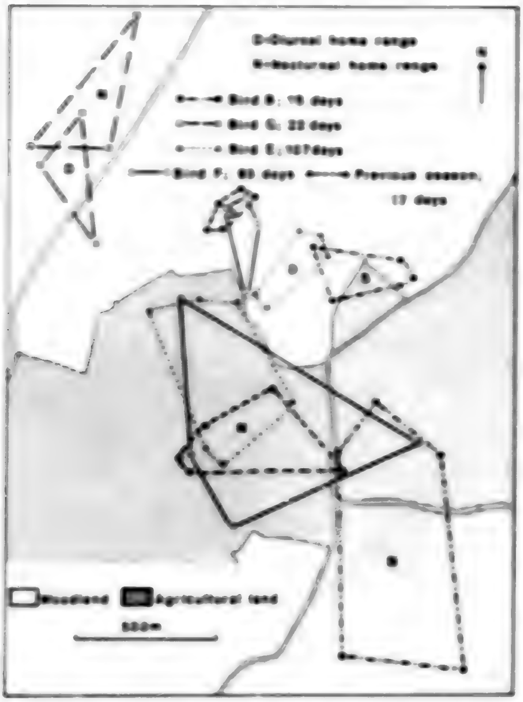

Fig. 2. Spatial distribution of the diurnal and nocturnal home ranges of 4 radio-marked woodcock on the study area, including the diurnal and nocturnal home range of bird F from the previous season (1978–79).

that the birds might have been roosting there, as clearcut areas are frequently used as roosts at night during the breeding season (G. Hirons, personal communication). After the third night these birds, in common with the other radio-marked birds (except for Bird G), adopted regular movements at dawn and dusk between daytime cover and nighttime fields. Bird G was radio-marked on 14 November 1979 and never left the woodland area during the 22 days it was monitored but frequented an area of thicket-stage woodland both day and night (Fig. 2). This bird, however, changed position regularly at dawn and dusk in common with the other birds. Since it was an immature, such behavior suggests that it may have been bred locally and had not yet acquired the necessary stimulus to move to fields at night.

Crepuscular Movements

The crepuscular movements of 12 radio-marked woodcock were recorded at dawn and dusk as the birds flew between daytime cover and nighttime fields (Table 2). At dawn the mean distance flown was 659 ± 346 m, with adults averaging 784 ± 345 m and immatures 488 ± 266 m. Similarly, at dusk the mean distance flown was 654 ± 346 m, with adults averaging 785 ± 345 m and immatures 467 ± 249 m. The difference in mean distance flown by adult and immature woodcock was statistically significant ($P < 0.001$).

The flight distances recorded at dusk by woodcock in this study were intermediate between those recorded by Hirons (1980) at two sites in England (Lanarth Estate, Cornwall, mean 444 ± 388 m, range 30–1,370 m; Whitwell Wood, Derbyshire, mean 1,035 ± 584 m, range 150–2,125 m).

Multiple flights (i.e., when birds landed on a field, remained for a few minutes, and then flew to a new position) occurred on 1% of dawn flights and on 3% of dusk flights.

Diurnal and Nocturnal Changes in Location

The incidence and mean distance of diurnal and nocturnal changes in location of 12 radio-marked woodcock are given in Table 2. On the basis that locations were recorded at the beginning and end of the diurnal ($n = 457$) and nocturnal periods ($n = 428$), the radio-marked woodcock studied here altered their nocturnal positions regularly (31%) and their diurnal positions less frequently (5%; Table 2). Hirons (1980) reported that in Cornwall, radio-marked woodcock that used small fields at night (<2.5 ha) moved to adjacent moorland for lengthy periods during the night, whereas two other radio-marked woodcock using much larger fields (>7.5 ha) spent the entire nocturnal period in these fields. Certainly in the present study Bird C, which used the largest pasture field (7.3 ha), showed the smallest number of nocturnal changes in position (16%), whereas birds E, I, and J, which were using smaller pasture fields (2.3 to 4.4 ha), changed position more frequently (between 30 and 43%). Other factors apart from field size, such as weather conditions or the presence of predators, can induce changes in nocturnal position. Snow and frost, for instance, cause more frequent movements as the birds search for unfrozen feeding areas (Hirons 1980;

Table 2. Mean distances (± SD given in parentheses) flown at dawn and dusk and incidence of diurnal and nocturnal changes in location shown by 12 radio-marked woodcock.

Birds and age	Mean distance (m) flown at		Diurnal period			Nocturnal period		
	Dawn	Dusk	Days checked	Location changes[a]	Distance moved (m)	Nights checked	Location changes[a]	Distance moved (m)
Adult								
A	427 (166)[b]	414 (163)	0	0	–	14	6 (43)	140 (64)
B	1,092 (361)	1,107 (314)	7	0	–	8	2 (25)	380 (368)
C	1,136 (244)	1,151 (229)	98	0	–	79	13 (16)	352 (311)
D	706 (498)	597 (467)	9	0	–	8	3 (37)	210 (78)
E	473 (141)	470 (152)	74	5 (7)	82 (25)	70	21 (30)	253 (139)
F	738 (113)	756 (102)	76	4 (5)	72 (22)	53	18 (34)	161 (56)
Immature								
G	207 (163)	160 (126)	8	1 (12)	170	6	0	–
H	245 (306)[c]	273 (324)	10	1 (10)	105	7	0	–
	220 (197)[d]	262 (239)	3	0	–	7	1 (14)	60
I	718 (140)	692 (155)	91	7 (8)	86 (50)	84	36 (43)	263 (185)
J	264 (96)	268 (102)	67	4 (6)	78 (35)	71	23 (32)	195 (110)
K	279 (290)	318 (251)	6	0	–	9	6 (67)	305 (192)
L	630 (244)	591 (180)	10	0	–	18	4 (22)	190 (74)

[a] Numbers in parentheses indicate percent.

[b] Excludes two return flights to other areas of daytime cover, 7.86 and 7.95 km distant.

[c] Distances between daytime cover and clearcut area (N = 6).

[d] Distances between daytime cover and nighttime fields (N = 12).

Wilson 1980), but during the winter under discussion periods of frost and snow were short and infrequent.

In daytime cover, by contrast, only six radio-marked woodcock were recorded as changing their locations on 22 occasions (5%). However, by monitoring the activity of radio-marked birds continually in daytime cover, activity was shown to be highly variable (from < 30 to > 70% of the diurnal period) among individual birds on the same day and for the same individual from day to day (Wilson, unpublished data). Hirons (1980; G. Hirons, personal communication) reported that woodcock in Cornwall were active in cover in 25% of the 5-min periods he monitored in 1978–79 and 18% in 1979–80, with a tendency for birds to be more active in the period before midday and immediately before the evening flight.

Although the factors that determine the degree and pattern of activity shown by radio-marked woodcock in daytime cover remain obscure, directional movement appears minimal. The detection of such movement will always be limited by the accuracy of the technique used in determining the exact location of the radio-marked birds.

Local Movements

Ring recoveries in the present study (Wilson 1980) have indicated that a small number (1.9%) of woodcock move locally (i.e., after being banded in the study area, they have been recovered within 10 km of it). Radio-marked birds have also shown this tendency to move locally. In the previous winter, one bird used a streamside strip of scrub 2.3 km from the study area (Wilson 1980) as did Bird A in the present study (4.15 km). On two further occasions, Bird A also moved about 8 km to areas of daytime cover, only to return to its home-range area at night. Bird F disappeared on three occasions during the diurnal period, to reappear on the fields at night shortly before it migrated. Local movement is therefore a definite if minor constituent of the overall winter behavior pattern. To date, there have been only two ring recoveries (Wilson, unpublished data) to suggest that woodcock

Table 3. *Dawn and dusk flight times (from December 1979 to March 1980) of 6 adult and 6 immature radio-marked woodcock in relation to sunrise and sunset under different cloud conditions. Data are given in minutes before sunrise or after sunset with the values representing mean ± standard deviation. Numbers in parentheses indicate sample sizes.*

		Cloud cover		
Period	Age	0–1/3	1/3–2/3	2/3–Total
Dawn	Adult	57.9 ± 9.9 (46)	48.8 ± 9.4 (27)	42.7 ± 9.1 (56)
	Immature	51.7 ± 5.2 (31)	45.7 ± 4.1 (19)	38.2 ± 7.0 (35)
Dusk	Adult	49.7 ± 7.7 (36)	44.8 ± 6.5 (43)	33.6 ± 8.2 (105)
	Immature	44.5 ± 5.3 (29)	41.7 ± 4.1 (36)	34.4 ± 5.4 (54)

choose alternate wintering regions either within the country (112 km) or in other countries (e.g., France).

Crepuscular Flight Times

The flight times of all 12 radio-marked woodcock were recorded and related to prevailing light conditions as characterized by three categories of cloud cover between December 1979 and March 1980 (Table 3). The 12 radio-marked woodcock moved at dusk to nighttime fields between 8 and 63 min after sunset. They returned at dawn to daytime cover between 73 and 19 min before sunrise. For adults, the time span of the dusk flight was 8 to 63 min and for immatures, 16 to 59 min after sunset; at dawn the corresponding figures were 73 to 27 min and 68 to 19 min before sunrise.

Both age groups of woodcock flew at significantly different times ($P<0.05$, t-test) at dawn and dusk under the three different cloud covers. Adult woodcock at dawn departed significantly earlier than immature woodcock ($P<0.05$, t-test) under cloud conditions 1 and 3. At dusk, adults flew later than immatures ($P<0.05$, t-test) under cloud conditions 1 and 2.

Under all categories of cloud cover, woodcock flew at lower light intensities at dawn than at dusk, as indicated by departure times; this probably reflects the generally brighter conditions prevailing in open habitat (fields) in comparison with closed habitat (woodland) at any one time. The difference is quite distinct, even allowing for the woodcock's habit of moving to woodland edges or openings before the dusk flight (marked and unmarked woodcock, personal observation). Nemetschek (1977) and G. Hirons (personal communication) report that breeding males display at lower light intensities at dawn than at dusk.

Home Range and Activity Center Sizes

Sizes of diurnal, nocturnal, and composite home ranges and of the diurnal and nocturnal activity centers for each radio-marked woodcock are given in Table 4. Mean diurnal and nocturnal home-range sizes were 8.4 ± 7.5 and 25.0 ± 10.8 ha, respectively. For adult woodcock, mean diurnal home-range size was 6.9 ± 7.1 ha, and mean nocturnal home-range size was 28.7 ± 7.1 ha. Similarly, mean diurnal and nocturnal home-range sizes for immature woodcock were 9.6 ± 8.3 and 21.9 ± 13.0 ha, respectively. All diurnal home ranges were within the woodland area except for Bird A, that located outside the study area (4.15 km) within a streamside strip of scrub (birch, alder, willow, gorse, and bramble), with its most distant locations 485 m apart. Nocturnal home ranges were confined predominantly to the agricultural land area, with the exception of the clearcut area which was used by three birds for short periods soon after they were radio-marked. Bird C never left the woodland area during the 22 days that it was monitored.

The total composite home range of 11 radio-marked woodcock in this study was 251 ha. Hirons (1980; G. Hirons, personal communication) reported that in Cornwall, in winter 1978–79, five woodcock had a composite home range of 146 ha, and in the same study area the following winter, six woodcock occupied 132 ha. Individual home ranges in the present study (average 44 ha; range 14.9 to 74.4 ha) were also

Table 4. *Sizes (in hectares) of diurnal, nocturnal, and composite winter home ranges (HR) and diurnal and nocturnal activity centers (AC) for 12 radio-marked woodcock (1,119 diurnal and 1,110 nocturnal locations). Numbers in parentheses indicate percent of locations used in defining activity center sizes.*

Birds and age	Diurnal		Nocturnal		Composite HR
	HR	AC	HR	AC	
Adult					
A	2.2	1.5 (67)	26.0	8.5 (68)	35.8
B	17.7	0.6 (73)	31.7	4.2 (67)	74.4
C	0.9	0.2 (96)	31.9	1.2 (68)	61.3
D[a]	10.5	0.8 (74)	32.5	2.1 (80) 0.7 (70)	33.1
E	3.9	0.1 (72)	16.0	3.9 (69)	30.0
F[b]	1.7	0.2 (74)	31.3	2.1 (79)	54.5
Immature					
G	5.7	0.6 (70)	5.5	0.7 (75)	12.1
H[a]	18.8	0.2 (67)	26.0	0.6 (68) 2.3 (72)	37.7
I	3.4	0.2 (79)	31.8	2.6 (70)	64.2
J	0.6	0.2 (71)	12.8	1.0 (71)	14.9
K	8.1	–	40.0	–	44.1
L	20.7	0.2 (81)	15.2	1.5 (79)	64.8

[a] Woodcock that used two nocturnal activity centers.

[b] Corresponding data for bird F (as an immature) from the previous winter (1978–79): 0.1, 0.1 (69), 10.5, 1.5 (77), 35.6.

much larger than those reported for England (average 21.4 ha; range 6.8 to 32.8 ha). Comparisons between nocturnal and diurnal home-range sizes were not possible. The smaller individual and overall composite home ranges in England presumably reflect the shorter average monitoring periods there (29 days compared with 59 days in Ireland), as individual home-range sizes in the present study continued to increase after 29 days (between 13 and 57%). Differences in the study areas are also important. The study area in Cornwall comprised small amounts of woodland cover (<40 ha) and moorland adjacent to an extensive field area that was predominantly permanent pasture (>95%). Permanent pasture, the preferred nocturnal habitat of the woodcock in winter, was more immediately available in Cornwall, as evidenced by the shorter average flight distances there (444 m) in comparison with those in Ireland (651 m) and northern England (1,035 m), where pasture fields are scattered among and outnumbered by cultivated fields.

Activity centers (Fig. 3) were demarcated within the diurnal and nocturnal home ranges of 10 radio-marked woodcock (Bird K was excluded due to insufficient data). The mean size of diurnal activity centers was 0.3 ± 0.2 ha, and that of nocturnal activity centers was 1.9 ± 1.2 ha. Mean sizes of diurnal and nocturnal activity centers for adults were 0.4 ± 0.3 and 2.4 ± 1.4 ha, respectively, and for immatures were 0.3 ± 0.2 and 1.4 ± 1.0 ha, respectively. Two radio-marked woodcock (D and H) used two nocturnal activity centers. Bird H first established a nocturnal activity center within the clearcut area for 9 nights before starting to use a second activity center on the nighttime fields. It returned again to the clearcut area for 2 nights before its transmitter malfunctioned. A similar pattern of activity center use was shown by Bird D. Both birds were monitored for short periods (D for 28 days, and H for 16 days), which suggests that each initial nocturnal activity center may have been related to a continuing period of adjustment to the transmitter package. One other radio-marked bird, Bird J, used the clearcut area for a single night, as did other unmarked birds (also see Wilson 1980).

The extent of overlap between the home ranges and activity centers of Bird F, first monitored as an immature bird in the winter season

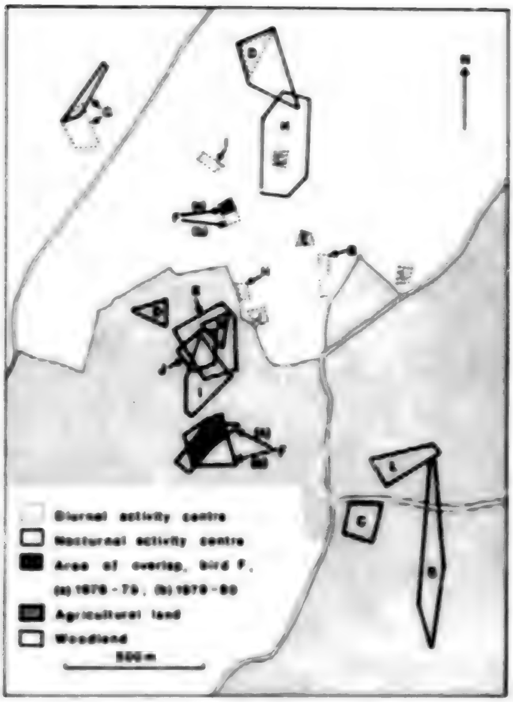

Fig. 3. Spatial distribution of the diurnal and nocturnal activity centers of 10 radio-marked woodcock. The degree of overlap in the diurnal and nocturnal activity centers of bird F from one season (1978–79) to the next (1979–80) is indicated.

1978–79 (Wilson 1980) and as an adult bird in the 1979–80 season, is shown in Figs. 2 and 3. Bird F was recaptured within 50 m of its original capture point and adjacent to its 1978–79 diurnal activity center. It moved that evening directly to the pasture field on which it had been monitored repeatedly during the previous winter. This single example underlines the high degree of fidelity to areas of daytime cover and nighttime fields and offers an explanation for the recurrence of woodcock in successive winter seasons, very often caught in the same pocket of a net set at the same net site (Wilson 1980).

Diurnal and Nocturnal Habitat Use

Modified habitat preference index values (Table 5) indicated that, by day, radio-marked woodcock selected young planted coniferous woodland (thicket stage) and, by night, pasture fields ($P<0.05$). Of the nocturnal locations of 10 radio-marked woodcock, 32% were situated in cultivated fields. When this habitat type is subdivided into three categories – (a) an open field area (77.8 ha) of winter barley or ploughed ground, (b) unploughed field margins about 1 m wide (3.2 ha), and (c) small, isolated wet marshes (2.4 ha) within some of these fields – it can be shown that categories (b) and (c) were preferred ($P<0.05$). At night, woodcock thus preferred permanent pasture areas, whether represented by pasture fields, unploughed field margins, or marshy areas. Very little use was made of the large areas of winter barley (see also Wilson 1980 and Hirons 1980), though personal observations during the present study showed woodcock "dibble" marks (probe holes) in these fields. The choice of permanent pasture is clearly

Table 5. *Habitat Preference Index*[a] *(HPI) and Modified Habitat Preference Index*[b] *(MPI) values for diurnal and nocturnal habitat types within the total composite home range of 11 radio-marked woodcock. Preference increases as MPI values approach HPI values.*

Habitat type	Area (ha)	Percent of total area	Diurnal HPI	Diurnal MPI	Nocturnal HPI	Nocturnal MPI
Thicket	68.4	27.2	2.72	2.72	0.08	0.03
Pole	31.1	12.4	1.93	1.06	–	–
Oak	0.4	0.2	1.0	0.09	–	–
Clearcut	14.1	5.6	0.30	0.05	0.46	0.08
Pasture	53.6	21.4	–	–	2.67	2.67
Cultivated	83.4	33.2	–	–	0.95	0.69
Totals	251.0	100.0				

[a] HPI = (percentage locations within habitat type/percentage habitat type within total composite home range).

[b] MPI = HPI × (number of radio-marked woodcock located in habitat type/total number of radio-marked woodcock).

linked with food availability, which is yet to be investigated.

All woodcock radio-marked in this study were mist netted at dawn as they entered daytime cover (i.e., planted coniferous woodland, thicket stage) because the capture technique could not be applied successfully elsewhere in the study area (Wilson 1980). Diurnal habitat preferences as shown by this study may therefore be biased in favor of thicket-stage plantations, since nine woodcock continued to use this habitat type as daytime cover. Two birds used nearby pole-stage plantations of Scots pine, and one used a streamside strip of scrub outside the study area. The pole-stage woodland occupied nearly 25% of the study area; by using dogs, it was demonstrated that unmarked woodcock used such areas as daytime cover where the ground vegetation was well developed, particularly beneath pines and larches. Coniferous plantations may be at their most suitable as daytime cover for woodcock at two stages: (a) at the thicket stage and (b) at a later stage (pole/mature) when timber removal allows greater light penetration for ground vegetation to reemerge or reestablish itself. This latter stage is reached much earlier under pines and larches than under spruces and firs. Plantations in the phase intermediate between (a) and (b) have been shown to hold few woodcock (Wilson 1980).

Wintering Strategy of Woodcock

The recapture of woodcock in successive seasons (13.9%) has been reported for four study areas over a 4-year period (Wilson 1980). Moreau (1972) discussed the recurrence of certain migratory species of the orders Passeriformes and Charadriiformes on their wintering grounds in Africa and states that "clearly the evidence for pin-point recurrence in successive seasons gives support to the opinion of Isakov (cit. Salomonsen) that 'most species of birds form minute so-called elementary populations. The members of these populations not only breed in the same limited area but follow the same migration route and winter in the same area.' "

Wintering site constancy in Passerines has been linked to a plentiful supply of available food (Finlayson 1980). The advantages of returning to a wintering area with a known food supply must be great. But year-to-year differences in, for example, weather conditions, farming practice, or numbers of birds can alter the available food supply, thus influencing whether a bird will return to its previous wintering area or seek an alternate one.

Evidence has recently become available on the fidelity of woodcock to breeding areas from season to season (G. Hirons, personal communication). Through the present study, the woodcock's habitual use of restricted wintering areas within one season, for the duration of that season, and in successive seasons has now been established. Evidence of search for alternative wintering sites, excluding local movement (<10 km), remains minimal, and as yet no direct evidence exists that periods of severe weather within a winter period stimulate "cold weather movements" of woodcock. The woodcock's need for an essentially frost-free environment to obtain its food during the winter probably governs its choice of wintering area. Familiarity with its wintering home range, acquired in its first season, then influences its choice in successive winters. It is probable, therefore, that sedentary behavior, coupled with the species' ability to increase weight rapidly in early winter (Rochford and Wilson, this volume), will assist survival, particularly in any subsequent periods of severe winter weather.

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Comparative Breeding Behavior of European and American Woodcock

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Abstract

The courtship displays and mating systems of *Philohela minor* and *Scolopax rusticola* are compared. Male *Philohela* are apparently promiscuous and display solitarily above small forest openings, areas which they defend against other males and in which mating takes place. Male *Scolopax* are successive polygynists; they defend neither an exclusive nor a specific area to which females are attracted, but instead perform extensive display flights above the forest canopy in search of females. When a receptive female is found, the male accompanies her constantly for several days prior to clutch completion before resuming display flights. The evolution of the polygynous mating systems found in these two species, and the ecological factors that may have favored the observed differences, are discussed. We believe that more research is needed, particularly on the behavior and significance of subdominant males.

Counts of displaying males are used to monitor population trends in the American woodcock, *Philohela minor*, and to estimate densities of breeding European woodcock, *Scolopax rusticola* (e.g., Merikallio 1958). However, because our understanding of woodcock breeding systems is so fragmentary, the reliability of these methods is difficult to assess (Owen 1977; M. Shorten, personal communication). The present paper summarizes what is known of the breeding behavior of both species and identifies gaps in our knowledge. The aspects considered are mating system, courtship displays, breeding season, and breeding habitat. Our intention is to generate ideas for further research from which should stem improvements in the methods used to assess woodcock populations in the breeding season. In addition, we consider the ecological factors that may have favored the differences observed between the polygynous mating systems and courtship displays of the two species, and we speculate on their occurrence within a family (Scolopacidae) in which monogamy is the usual condition (Lack 1968).

Information on the breeding behavior of *Scolopax* is taken mainly from a recent (and continuing) radiotelemetry study in Derbyshire, England (Hirons 1980; Hirons and Owen 1980), while that for *Philohela* is our own interpretation of the extensive literature on the subject (see particularly Sheldon 1967).

Mating System

Unlike most shorebirds (Lack 1968), neither *Scolopax* nor *Philohela* is monogamous. Paternal care is absent in both species, and there is no evidence of territorial behavior by females or broods (Sheldon 1967; Hirons 1980).

Male *Scolopax* are successively polygynous but, in contrast to other waders with polygynous mating systems, they do not defend either an exclusive or specific area to which females are attracted and in which mating or nesting (or both) take place. Instead, males display solitarily over extensive areas in search of females with which to mate. When a receptive female is found, the male remains with her constantly for a short period, usually 3–4 days, before resuming display flights. As in many other polygynous species (Wiley 1974), a proportion of first-year males, probably variable from year to year, do not participate in breeding activities (at least in Britain). There appears to be significant variation in the success of individual male woodcock in locating and mating with females, which is apparently related to differences in their display performance (Hirons and Owen, unpublished data).

Philohela differs from *Scolopax* chiefly in that males display on specific areas, termed singing grounds, which are defended vigorously against other males and to which females are attracted for mating. No pair bond is formed, and contact between the sexes is apparently limited to copulation, which takes place only on singing grounds (Sheldon 1967). It appears that some males mate with more than one female, but there is no published information on variation in mating success between males in possession of a singing ground. Many studies, however, have demonstrated that if the occupant of a singing ground is removed, replacement occurs rapidly and that there may be as many as three noncourting, or subdominant, males for each displaying male (Owen 1977). The way in which these dominant–subdominant relations are established is unclear, and both categories include first-year and adult males. In Michigan, the age ratio of courting males captured on singing grounds changed through time, with adults predominating early in the breeding season (Whitcomb and Bourgeois 1974), but no similar seasonal shift occurred in West Virginia (B. Shissler, personal communication) or New Brunswick (D. Keppie, personal communication). Thus there is no concrete evidence that older, more experienced males dominate breeding activity, as apparently occurs in *Scolopax*. However, subadults occupy marginal sites more often than adults (D. Keppie, personal communication) and may more readily colonize newly created singing grounds (Dunford and Owen 1973).

Our interpretation of these data is that male *Philohela* are promiscuous and display solitarily, so their system of singing grounds is probably analogous to the dispersed leks characteristic of some wader species (Lack 1968).

Courtship Display

Scolopax

Male *Scolopax* perform extensive display flights, termed roding, above the woodland canopy. When roding, birds fly in a distinctive manner, quite fast (about 32 km/h) (Nemetschek 1977) but with a peculiar, slow wing action like that of owls, and they call repeatedly. Two quite different notes are used in conjunction: a guttural, croaking sound repeated three to five times in quick succession followed immediately by a shrill, far-carrying "peetsch" note; the whole call sequence lasts 1–2.5 s.

Over most of its breeding range (temperate Eurasia), *Scolopax* rodes at dusk and, less intensively, before dawn, from late February to early July or later. At the species' northern limit, around 69° N in Scandinavia, roding can be observed at any time during the 24 h (Marcström 1974). The number of flights observed and the length of display periods increases through the season, reaching a maximum around the summer solstice, at which time in Britain the evening display in any one area usually lasts for about 50–70 min and between 20 and 30 observations of roding birds can often be made. The same basic pattern of increasing display activity with season is also shown by marked birds, but with much individual variation.

Roding birds are seldom continuously in the air for more than 20 min (maximum yet recorded, 43 min), and usually an individual's evening display consists of 2–4 flights averaging about 6.5 min each (Hirons 1979). Most birds display for about twice as long in the evening as in the morning, and the maximum recorded period of display by one individual in a 24-h period has been 64 min. Marked males have displayed throughout the entire season (i.e., more than 4 months), but there is some evidence that not all roding males do so.

Display begins progressively earlier in relation to sunset and sunrise as the season proceeds. In England, roding takes place in the evening at average light intensities between 15.6 and 6.7 lx in early march but between 398.1 and 1.4 lx in June. In the morning, roding usually ceases about 45 min before sunrise, when light intensities (usually <0.3 lx) are even lower than those at which roding ends in the evening. The height of display flights is also influenced by light intensity. Initially each evening the birds fly well above the tree canopy ($\bar{X} = 22$ m) (Nemetschek 1977), but with declining light intensity, the height of display is reduced to just above that of the canopy.

Roding birds tend to concentrate their activity above clearings, paths, and other woodland openings, and individuals frequently fly over such places several times during each display period (maximum recorded: 11 observations of one individual during one evening). Aggressive interactions occur frequently when roding males meet, but this does not prevent many birds from displaying over the same area. Individual roding ranges in England are often more than 100 ha in extent, and marked birds have been observed displaying over points 3 km apart on the same evening and 6 km apart in the same week. It is likely, however, that the length and orientation of roding routes is influenced by the extent of woodland areas, by topographical features such as paths and clearings and, perhaps, by the density and distribution of females.

Roding males exhibit a high degree of fidelity to particular areas: [illegible] 13 roding males caught in a 170-ha wood in England were retrapped there the next summer.

There are several accounts of apparent courtship behavior on the ground that may describe the precopulatory display of *Scolopax* (Shorten 1974). Observations of captive birds suggest that fluffing of the plumage, shivering movements of drooped wings, and rapid trembling of the fanned, raised tail serve as the precopulatory display of the male (Glütz von Blotzheim et al. 1977; V. Marcström, personal communication; G. Hirons, unpublished data).

Philohela

In the breeding season, male *Philohela* perform courtship displays at dawn and dusk on singing grounds. These grounds range from 0.1 to more than 40 ha and consist of old fields, forest cuttings, bogs, and other openings (Owen 1977). In Maine, singing begins soon after the birds arrive from winter quarters in late March and continues until early June.

From the singing ground, the male performs a series of display flights each lasting about 55–60 s. In these, he rises vertically up to about 80 m (Sheldon 1967) before descending in spirals; during descent, the specially modified outer three primaries produce a characteristic twittering sound, which is accompanied by vocal chirps. The aerial display is followed by a ground display in which he gives a series of "peent" calls, each preceded by a faint "tuko" note. This repertoire is repeated 10–20 times during the display, which lasts from 30 to 60 min (Pettingill 1936; Sheldon 1967). Aggressive encounters with intruders are common, involving chases and "cackle" calls, and males occasionally spend an entire courtship period defending their territory (Westfall 1954).

Evening display begins at light intensities between 53.8 and 2.2 lx (Sheldon 1967:55), which is much lower than for *Scolopax* at the peak of its roding activity. As with *Scolopax*, there is a latitudinal influence on the length of the courtship period (Sheldon 1967:55), with males in New Brunswick singing about twice as long (45 min) as birds in Maryland (20 min). This difference may be related to the length of the twilight period. However, seasonal trends in *Philohela* display activity appear less marked than for *Scolopax*.

Displays at dawn are less synchronous than in evening, and the total display period is correspondingly about 50% longer (Sheldon 1967); we found no published information that compares individual dusk and dawn display performances.

In West Virginia, some territories were occupied daily for up to 3 months, but others were used only temporarily (B. Shissler, personal communication), suggesting that there are preferred singing grounds. D. Keppie (personal communication) came to the same conclusion from studies of the recruitment of males to singing grounds from which the dominant male had been removed. In the West Virginia study, many males remained dominant on the same singing ground for extended periods (up to 70 days), but some birds did change territories and some even became subdominant on other singing grounds.

Females visiting singing grounds allow mating by males with minimal precopulatory display and so may differ from *Scolopax* in this respect. In the presence of a female, male *Philohela* utter a series of low "tuko" notes, then approach with wings raised above the back, dropping them almost to the ground just before mating (Westfall 1954:31; Sheldon 1967:49).

Male *Philohela*, like male *Scolopax*, show high fidelity to previous breeding localities. Of 84 males retrapped by Sheldon (1967) in subsequent breeding seasons, 32% were retrapped on the same singing ground and 80% on singing grounds within 1.6 km of the original capture site.

Breeding Season

Scolopax has a very protracted breeding season as compared with that of *Philohela*. In Britain, generally the first eggs are laid in early March, the peak of laying is from mid-March to mid-April, and some clutches are found as late as August (Morgan and Shorten 1974). A similar pattern holds for Denmark (Clausager 1972). However, in an area intensively studied in England, the distribution of layings lacked this pronounced peak in early spring, perhaps because nests started early in the season are found most easily by casual observers. In this area, at least some of the clutches laid after late April were replacements. Females can also lay again after losing broods; in two such instances recorded, incubation of the repeat clutch began only 12 days after brood loss, which may indicate that some females can successfully rear two broods in a season.

The breeding season of the single-brooded *Philohela* is relatively short. Sheldon (1967) reported that 90% of the nests recorded in several studies were started within 4–5 weeks. In England, 93% of the clutches of *Scolopax* were started in the period 21 March–3 May (G. Hirons, unpublished data) and in Denmark, 90% were calculated to have been started over a 15-week period (Clausager 1972).

Habitat in the Breeding Season

Over most of its range, *Scolopax* breeds in extensive tracts of undisturbed deciduous woodland, particularly those having a combination of dry ground with a sparse herb layer (e.g., brambles, *Rubus* spp., or Dog's Mercury, *Mercurialis purpurea*) and wide paths or other openings that allow birds easy access to the forest. Typical habitats vary from large areas of hardwoods or mixed woods in the south of the woodcock's range to thin birch (*Betula* spp.) woods and scrub in the north. In Britain, young conifer plantations are also frequented, and in Scandinavia, mature coniferous forests.

Philohela is associated with earlier stages of forest succession than *Scolopax*. Prime habitat in the northeastern part of its range is provided by old farms reverting to forest. These areas contain young to middle-aged hardwoods, especially alder (*Alnus* spp.), openings, and abundant food. In the northwestern part of its range, the most favored habitat is aspen (*Populus* spp.) and birch forest less than 30 years old. Other favored habitats are recently logged or burnt areas, even when these are surrounded by extensive stands of conifers.

Discussion

Most northern scolopacids breed in open habitats. Nearly all are monogamous, with male involvement in incubation and brood rearing (Lack 1968), and males of most species defend territories for the purpose of mating, after which territorial behavior and courtship display cease (Miller 1979). In contrast, paternal care is absent in both woodcock species and the polygynous males display throughout the breeding season. Many aspects of woodcock social behavior and morphology can be viewed as secondary adaptations to their unique forest existence, and the differences in breeding behavior between woodcock and other shorebirds, and between the two species themselves, are discussed with this in mind.

Courtship Displays

Both woodcock species are sexually monomorphic, have highly cryptic plumage, and in the breeding season feed solitarily beneath the woodland canopy, all of which make contact between the sexes for mating difficult. To overcome this problem, both species have evolved conspicuous aerial displays accompanied by distinctive vocalizations. In both species these displays are performed only by males; in *Scolopax* the male ceases his aerial display for the duration of the pair bond, and in *Philohela* mating takes place only on a singing ground from which the aerial displays are given. Thus, there can be no doubt that the display flights in both species function primarily to attract females.

Philohela occupies earlier stages of forest succession than *Scolopax* and accordingly can make repeated, vertical display flights from the more abundant suitable openings, which can also be defended against other males. The presence of subdominant males around singing grounds, the rapid replacement of removed males, and the rapid colonization of newly created openings suggest that there is considerable competition between males for singing grounds. *Scolopax* is associated with more mature woodland, and this may have been one reason for the evolution of its extensive display flights above the tree canopy. Male courtship display around sunset and before sunrise occurs in related partly nocturnal species, such as the snipe, *Capella gallinago* (Tuck 1972) and the great snipe, *Capella media* (Lack 1968). The strong diel rhythms of display in the woodcock could have evolved to facilitate contact between the sexes by serving as a "temporal" address while also avoiding competition with the other sounds of woodland bird communities and perhaps also reducing the risk of predation.

Polygyny and Length of Breeding Season

Why most Scolopacidae should have evolved monogamous mating systems is obscure (Lack 1968; Wilson 1975:329). However, several factors have probably favored polygyny in *Philohela* and *Scolopax*. Advertisement and defense of exclusive areas of woodland containing resources of value to females would be difficult for a well-camouflaged shorebird not adapted to perching. In comparison with most species of waders, both woodcock species have extended breeding seasons and both will nest again if a clutch is lost. The optimum areas for nesting probably differ within and between breeding seasons according to conditions of ground cover and food availability, which are subject to meteorological influences. Female *Scolopax* almost invariably change locations between nesting attempts (personal observation). This mobility of females may have favored the evolution of the extensive display flights by male *Scolopax*, and makes defense by males of the females (harem polygyny) impossible. Paternal care is absent in both species – the nidifugous chicks feed themselves, at least after the first few days, and presumably in a woodland situation there would be little selective advantage (from improved detection or distraction of potential predators) if both parents attended the brood.

Extended laying seasons result in an excess of males over receptive females at any one time in the breeding season and are characteristic of many species with polygynous mating systems (Emlen 1976). In species where there is no long-term pair bond, this in turn will result in intensive intrasexual competition for mates, and high variance in reproductive success among males. Furthermore, males should remain sexually active throughout the breeding season, as occurs in both *Philohela* and *Scolopax*.

In *Scolopax*, the extraordinarily long breeding season stems from a great asynchrony in the timing of egg laying caused by high rates of nest predation and frequent repeat layings (personal observation), and probably also from differential ability of females to accumulate the resources necessary for breeding. Although nonsynchronous arrival on the breeding grounds by females may also occur, it would be difficult to detect.

Why the breeding season of *Philohela* is so much shorter than that of *Scolopax* is a puzzle. In Britain, 67% of *Scolopax* nests started hatch at least one chick (Morgan and Shorten 1974), which is identical to the proportion of successful *Philohela* nests in Maine (Mendall and Aldous 1943). In *Scolopax*, the termination of roding each year, and by implication breeding, occurs later in wet summers (Saari 1979; Hirons and Owen, unpublished data). This extension of the breeding season may be because broods suffer higher mortality in wet seasons, resulting in more repeat nestings, or alternatively because earthworms are more readily available and the birds are thus able to continue breeding later. The latter explanation definitely applies to blackbirds (*Turdus merula*) and song thrushes (*Turdus philomelos*) that breed in the same geographical areas and depend on earthworms for food. It is plausible that earthworms become less readily available and feeding conditions correspondingly poorer earlier in the summer in the habitats and regions occupied by *Philohela* than in those occupied by *Scolopax*.

In both *Scolopax* and *Philohela* there is probably considerable variance in mating success among males. Some male *Scolopax* do not display at all (personal observation) or display only when other males have been removed (Marcström 1974), and even among displaying males some are much more successful at finding mates than others (Hirons 1980; personal observation). There may be as many as three noncourting *Philohela* males associated with each singing ground, and some presumably unsuccessful but displaying males change singing grounds during the breeding season. Subdominance associated with a singing ground may be a strategy employed by less dominant males to increase their chances of mating by being in a position to rapidly replace the territory owner during that or subsequent breeding seasons; it is possible that singing males are more vulnerable to predators than the population at large. Also, subdominant males may opportunistically steal mates while the resident male is displaying or interacting with other males.

In both species, choice of mate, initially at least, is probably the prerogative of the female. In *Philohela*, mating takes place only on a singing ground, and females are free to move from one singing ground to another. Female *Scolopax* are believed to give an advertising call which, when heard by the flying male, causes him to alight next to her (references in Hirons 1980).

Intense intermale competition and female choice of mate are primary determinants in the evolution of lek-mating systems (Emlen 1976), in which males increase their attractiveness to potential mates by congregating to display on arenas or leks. Among waders, communal displays are performed by ruffs (*Philomachus pugnax*) and male great snipe, both of which inhabit more open country than woodcock. In the forest habitats occupied by woodcock, suitable openings for arenas which are also safe from the risk of predation are likely to be in short supply, or far removed from suitable feeding and breeding areas. Neither *Scolopax* nor *Philohela* move around beneath the woodland canopy at night in the breeding season (personal observation), and it is likely that the risk of predation would counteract selection for closely aggregated displaying males. However, it is also likely that areas of high roding male density (*Scolopax*) and groups of singing grounds (*Philohela*) attract more females than isolated displaying males.

Intersexual Selection

In neither species of woodcock is the mating system resource based (Cronin and Sherman 1976; Trivers 1976), which makes discrimination of male quality more difficult for females, and this may have resulted in some of the differences observed between the breeding behavior of the two species. One way for females to determine the quality of potential mates is by their success in intermale competition. In *Philohela*, intermale competition for singing grounds is great, only a proportion of males posess singing grounds, and these are defended vigorously against other males. Thus, females are able to select males from a group of "winners"; correlated with this ability is the lack of a pair bond and virtually no precopulatory display (see below). This prior sorting may be important in *Philohela*, which has a shorter breeding season than *Scolopax*, since it allows rapid choice of mate and an early start to nesting. In addition, since females are selecting males principally on the basis of their possession of a singing ground, seasonal trends in display activity would not be expected (cf. *Scolopax* below).

Female *Scolopax* have an extended laying season, and usually change breeding localities (and hence mates) between nesting attempts. Perhaps because of subdominance, some males (mainly first-year males) do not display. The remaining males display but do not defend territories containing resources of value to the female, and although some males display more than others (and the females may distinguish these males by voice) (G. Hirons, unpublished data), the results of intermale competition are less tangible than in *Philohela*. Hence, it may be more difficult for female *Scolopax* to gauge male quality quickly; this may be the reason for the temporary pair bond and more elaborate precopulatory display found in *Scolopax*, which allow the female a finer discrimination of male quality. An alternative explanation for the existence of a pair bond in *Scolopax* could be mate-guarding by the male, but this should be balanced against the male's loss of valuable time in which other females could be inseminated (Wilson 1975). Regardless of the reasons, a mating system that includes the formation of a pair bond lasting several days would be less likely to evolve in *Philohela*. Males could not afford to relinquish their singing ground or lose time in which to mate with other receptive females, especially given the shorter, more synchronous breeding season of *Philohela*.

Female *Scolopax* appear to select males initially on the basis of their roding ability, i.e., the males which display longest (personal observation). Therefore, if other considerations allow, males should always display for the maximum period possible, which may explain the seasonal trends in male roding activity. Early in the season, during cold weather, apparently even the fittest males can rode only for short periods (personal observation).

Census Methods

Estimating the number of courting males in the breeding season will always be far easier for *Philohela*, which display on small, discrete singing grounds, than for *Scolopax* where several males perform songflights over the same extensive areas. For *Scolopax*, census of roding males will probably have to be based on the proportion of marked to unmarked birds (radio-tagged or otherwise distinguishable individually) in the population. However, for both species there still remain the problems of relating the number of courting males to the number of breeding females and of whether this ratio varies from year to year or between areas. Yet given a more complete understanding of woodcock breeding systems, this problem might appear less intractable or less important than it does at present, and we discuss specific areas where our knowledge is deficient.

Future Research

In reference to *Philohela*, some specific questions that need an answer: How much variance in mating success is there between males in possession of singing grounds and what factors influence this? Possibilities to be investigated are the position of the singing ground in relation to other singing grounds and their relation to prime brood rearing and feeding habitats, variation in male display performance, age of displaying male, and density of singing grounds. More data are needed on individual occupation of singing grounds, both within and between seasons. Are males in possession of singing grounds exposed to higher predation? What is the effect on total population size of manipulating the habitat to increase the potential number of singing grounds?

Little is known about female behavior in relation to singing grounds. In particular, how promiscuous are females? What is the relation of the location of nest sites of individuals to the place where mating occurred? Are there seasonal trends in breeding success as evidenced by predation rates on nests or the growth and survival of chicks?

In *Scolopax*, the outstanding problem is why some males display more than others and some not at all. Removal of dominant males and its consequent effect on the display behavior and mating success of the remaining males should help to answer the question. A similar experiment with marked males should be conducted with *Philohela*.

An additional area of interest in *Scolopax* is the wide variation in body weights of individuals of both sexes and its effect on the timing of laying and male courtship performance. Allied to this is the variability in food abundance and its influence on body condition and length of breeding season.

Clearly, we have a long way to go to achieve a complete understanding of the breeding behavior of either species, but it is well to remember that progress in this direction will be achieved only if the relevant questions are posed initially. This presents a challenge to all of us.

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Symposium Summary

by

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The 7th American Woodcock Symposium, dedicated to the memory of Roger Latham, is drawing to a close. We have listened to an array of presentations ranging in scope from narrow technical issues to complex relations between woodcock and their environments. The participants have come from many parts of the United States and Canada, and our colleagues from Europe have added a special flavor to the meeting. Each of the speakers is an expert in his own right, but I am sure all of us benefited from the exchange of ideas and information that has taken place during the last 3 days.

I have the privilege now of recapping some of the highlights of this symposium, and the opportunity of offering an opinion or two about the direction woodcock research and management activities should take in the future.

Bob McCabe is an old friend, and his keynote address was vintage McCabe – 100 proof, smoothed by almost four decades in the barrel. He took us back to the beginning – back to the early days when our knowledge of the woodcock was anecdotal and when scientific wildlife investigation was in its formative stage. He traced the development of knowledge about the woodcock; the learning process has not been easy or without obstacles. However, we have come a long way, and Bob helped put the current proceedings in their proper perspective. I particularly appreciated his comments that woodcock populations are likely unaffected by current levels of exploitation, that it would be folly to initiate a range-wide banding program to study population dynamics, and that we should avoid conducting "so-what" research and focus attention on solving management problems. I wish I could share his optimism that woodcock habitat is reasonably secure; serious problems are emerging in wintering areas. His comments about promoting interests in woodcock hunting were right on. People should enter the sport of their own volition rather than because someone pointed out the existence of an underutilized natural resource.

In the introductory session, John Tautin provided a brief history of the evolution of procedures used in analyzing woodcock singing-ground survey data. He believes that field procedures are satisfactory but analytical methods need to be improved. His preliminary evaluation suggested that the effect of observer change on population index calculations is negligible, and that the recommended starting times for conducting woodcock surveys are appropriate.

Dwyer and Nichols discussed results of their woodcock banding studies. Their data suggested that survival rates of females are higher than those of males, and higher among adults than young. They expressed concern for the lower overall survival and production-rate estimates of the Eastern population. Although the sample sizes were small and refuge banding sites may be less than representative, their findings suggest that significant differences exist between the Eastern and Central populations.

The next four papers, constituting Technical Session I, concerned some biological and behavioral characteristics of the American woodcock. We still have much to learn about the basic biology of this species.

Andy Ammann discussed his pioneering technique for determining the hatching dates of woodcock chicks using bill-length measurements. The accuracy of this method was confirmed, and Andy commented on the duration of its reliability with increasing age of the chick.

Shissler et al. described results of color banding individual woodcock for subsequent identification and study. Reflective color bands were placed on a large sample of birds in West Virginia, with a high rate of individual identification. They pointed out some potential applications associated with a marking technique that allows observation of the activities of undisturbed woodcock.

Larry Gregg focused attention on the woodcock singing-ground survey and its potential as an indicator of habitat quality and availability. Larry suggested that on his study areas in northern Wisconsin, a strong relation exists between the number of singing woodcock, the number of nesting hens, and the availability of habitat. Singing-ground survey data may have an unrecognized value as a means of monitoring breeding habitat trends. He noted that good breeding habitat is decreasing in Wisconsin due to normal forest succession, and emphasized the value of habitat diversity.

Weir and Graves recognized the potential of using individual characteristics of the peent call in studying territoriality of male American woodcock. Although differences exist among calls of individual males, they found that variations in the call of a single bird, overlap among birds, and experimental error made it difficult to accurately separate large numbers of males. However, they remained optimistic in concluding that sonographic analysis and behavioral clues used together may accurately determine individual use of woodcock singing sites over the course of the breeding season.

The second technical session shifted us from basic biological considerations of the woodcock to habitat structure and habitat requirements during courtship, nesting, and brood-rearing periods.

The initial presentation by Kinsley, Liscinsky, and Storm was the first of two papers using multivariate statistical techniques to identify and quantify some important habitat characteristics of woodcock singing grounds in Pennsylvania. By comparing old singing-ground sites with those currently in use, they demonstrated that plant community development gradually reduced the suitability of a singing ground. Quantitative methods may prove useful in describing initially suitable areas, determining if these areas become less useful to woodcock, and classifying suitable and unsuitable habitat.

Gutzwiller and Wakeley continued the discussion of woodcock singing-ground habitat. They described a use index for each singing ground and determined a high correlation between this index and the habitat variables of edge height, shrub density, and opening size. They pointed out the obvious benefit to wildlife managers of identifying the habitat characteristics that typify quality woodcock singing grounds.

Coon and his associates shed additional light on woodcock nest-site characteristics in Pennsylvania. They were able to identify nest sites on the basis of four habitat variables, and determined that the spatial distribution of sites on the study area was random. They emphasized the need to assess the relation between singing-male density and nest or brood density as a measure of the potential productivity of woodcock breeding habitat.

Dwyer, Derleth, and McAuley told us about some important aspects of woodcock brood ecology in Maine. They found smaller brood sizes in second-year females, annual variations in the sex ratios of fledged chicks, and no differences in survival of broods produced by second-year or older females. They also provided us with important data on habitat preferences in Maine between young and older broods. Key management considerations were discussed in light of their results.

Horton and Causey reported on a radiotelemetry program in east-central Alabama in which they monitored the activities of woodcock broods. They pointed out the reduction in association of brood members, including complete disassociation after the sixth week. This gradual adjustment of brood members to an independent existence was emphasized in relation to brood densities around selected fields.

The special session on the effects of current forest management and land-use trends on woodcock habitats was both stimulating and productive. Little information is available in the literature on this important topic. I believe this is the first time in this series of symposia that speakers have been asked to address a specific topic concerning the ecology and management of woodcock. It's a good move.

John Baird began the session with an excellent discussion of the changing forestland uses in New England and the Maritime Provinces. He cited four major trends in land use that will have varied effects on woodcock habitat: (1) continued loss of land to urban uses, (2) decrease in farmland reverting to forests, (3) intensified large-scale forest management, and (4) growing public awareness and influence in forestland management. He concluded by challenging wildlife managers to participate in land-use policy decisions that benefit wildlife in general and woodcock in particular.

Strauss and Gutzwiller continued and expanded upon the theme established by John Baird and emphasized the role of economics in wildife management. Man and wildlife are competing for use of land, and wildlife is often the loser. In Pennsylvania, and probably elsewhere in the Eastern Region, the decline in the woodcock breeding population index most likely reflects a combination of long-term changes in land use and normal ecological succession.

Carl Bennett described a major research program in Michigan aimed at gaining knowledge about the economics and best choice of procedures for managing forest wildlife habitat, and the public reaction to such programs. This rather spectacular effort, involving study plots of 23.3 km² (9 mi²), is yielding good information about the response of deer, ruffed grouse, and woodcock to clearcuts ranging in size from 25 to 75% of the cover. Woodcock appeared to benefit most from the largest cuts.

The third technical session extended the special session by emphasizing the response of woodcock to habitat management in various parts of the country.

Sepik and Dwyer took us back to Maine where habitat management techniques, applicable to both small landowners and large commercial forestry operations, were developed and evaluated. Strip clearcutting of diurnal cover increased summer use by adult females and juveniles when singing males were present. Firewood cutters created small clearings in hardwood stands that increased singing-male activity over previous levels. They presented some interesting findings on the relation of cleared areas to the age structure of courting males, and cited the importance of spring burning in woodcock habitat management.

Rabe and Prince described results of their work in northern Michigan. They emphasized the need to understand the spatial associations of singing-ground and diurnal cover in relation to woodcock use. They conceptualized woodcock habitat preference in terms of three critical components: food, diurnal cover, and singing grounds. They recommended that habitat management programs for woodcock give priority to production of food, followed by creation of diurnal cover and then of singing-ground habitat.

The last paper in this session, by Johnson and Causey, presented results of management studies in the South. They described the effects of prescribed burning of longleaf pine stands on subsequent woodcock use. Woodcock abundance was highest in the most recently burned stands. They concluded that fire could play an important role in converting southern pine stands to attractive habitat for woodcock.

In Session IV, attention shifted to reproduction and wintering habitat studies of the American woodcock in the southern regions of the United States.

Mason, Causey, and Lisano described development of a simple method for distinguishing breeding from nonbreeding females in wintering populations. Some females start sexual recrudescence while others remain quiescent during the winter months. They suggested that blood-serum characteristics might be useful in identifying and estimating the number of reproductively active woodcock.

Whiting and Boggus discussed reproductive variables of woodcock wintering in East Texas. Courtship flight activity peaked by mid-February when the majority of all males had attained sexual maturity. Generally, adult males achieved testes maturation about 2 weeks earlier than subadults. Some females achieved sexual maturity by late January. However, evidence suggested that only adult hens initiate nests in East Texas.

Connors and Doerr discussed the use of agricultural fields by woodcock in southern wintering areas. In North Carolina, they found that roosting woodcock preferred certain types of agricultural fields over others, and distributed themselves in small clusters or aggregation of birds. A local banding program established both the breeding-ground origin of their birds and the tendency of birds to home to specific fields in successive years.

In the last paper of this session, Boggus and Whiting described habitat variables that typified preferred feeding sites of woodcock in young pine plantations, and suggested that vegetation was more important than soil as a factor influencing foraging activities. Key management considerations were discussed for this region.

In the final session of this symposium, our colleagues from Europe provided a series of presentations summarizing their work on the European woodcock.

Heribert Kalchreuter summed his thoughts on the history of European woodcock populations, especially with regard to population fluctuations and breeding-range expansion. He highlighted extension of the breeding range into the British Isles during the last century, which corresponded with a population decline in Eastern Europe. About 50 years ago, the population trend reversed itself. He discussed many interesting hypotheses and their validity in light of historical and current information and suggested that added attention be given climatic factors.

Rochford and Wilson described efforts in Ireland to develop a reliable method of external sex differentiation. They analyzed various morphological characters from internally sexed birds. Unfortunately, normal variation resulted in an overlap of measurements and made accurate separation impossible.

Wilson discussed an interesting radiotelemetry study of wintering birds. Woodcock in Ireland preferred young coniferous woodlands during the day and pasture fields during the night. He expanded on the habitual use by woodcock of restricted wintering areas within one season, for the duration of the season and in successive seasons.

Hirons and Owen compared the courtship displays and mating systems of the American and European woodcock. They identified differences between the two species and discussed the ecological factors that may have favored the evolution of polygynous mating systems in both birds.

This concludes my remarks highlighting material presented at this symposium. The next few minutes will be spent discussing some of the key issues affecting the future of woodcock management in North America.

Management Needs

The main information needs for managing most species of hunted wildlife, including woodcock, are generally well recognized. Managers need to know something about:

- the size of breeding populations,
- the productivity of populations,
- annual harvest rates, and
- annual survival rates.

Ray Owens and his committee described these needs in their 10-year management plan recommended in 1975 at the 5th Woodcock Workshop. There is little need for me to expand here upon the nature and importance of these information requirements, but I do want to offer some suggestion about how they may best be met.

The cooperative singing-ground and wing-collection surveys will be continued for the present but, as John Tautin pointed out earlier, improvements are needed in analytical techniques. We need a better understanding of the value of the annual singing-ground survey as a means of monitoring woodcock abundance.

Despite major long-term banding efforts at a few locations, we still are uncertain about basic woodcock population structure and dynamics. There appears to be no simple way of obtaining the needed information. Recent technical advances in the statistical analysis of banding data indicate that the level of banding effort needed to produce reliable information is far beyond our current capabilities. Realistically, there is little point at this time in pursuing a rangewide preseason banding program to acquire the necessary information about woodcock population dynamics.

What alternatives do we have? It appears that we must continue to rely upon indirect means of monitoring populations, and it is clear that a better procedure is needed for acquiring harvest information. At this time, the only practical means of gathering the kinds of data needed appears to be some form of a rangewide system that provides opportunities for contacting woodcock hunters. In my opinion, the best method of doing this is through use of a mandatory permit required of all migratory bird hunters. Use of such a permit would provide names and addresses of these hunters and thus an opportunity to draw statistically valid samples for survey purposes. The survey should be designed to produce information about the size, timing, and distribution of harvests; the extent of crippling; the productivity of various populations; and the relative importance of populations to harvest. It would then be possible to make direct evaluations of the reliability of the singing-ground survey. The degree of public interest in woodcock hunting in various regions could be measured. In short, well-designed mail-questionnaire and parts-collection surveys can provide most of the information generally recognized as being important for managing a hunted wildlife resource.

The U.S. Fish and Wildlife Service endorses the concept of such a data-gathering program. A good deal of state support has emerged nationwide, but it is less than universal. We are working with the International Association of Fish and Wildlife Agencies to find means of developing an acceptable permit system. Both the Service and the International Association are interested in a program involving all migratory game birds.

Efforts should continue to determine how habitat can be managed in a cost-effective way. How can habitat best be manipulated to provide the early successional stages of vegetation that benefit both breeding and wintering woodcock and many other species of forest wildlife?

Woodcock habitat research has traditionally centered on the breeding grounds. This work is needed and should continue, but there is an increasing need to focus attention on the wintering grounds. Bottomland hardwoods are being cleared at an alarming rate to make way for agricultural, industrial, and other uses of the land. Losses along the Mississippi Delta are of particular concern, but the problem is widespread. We need to identify where woodcock habitat is declining and develop programs whereby the requirements of wintering birds can be met in the future.

It will be a real challenge to save enough habitat for wintering woodcock. Perhaps the best way will be to promote habitat preservation on an ecosystem basis. Many migratory birds, both game and nongame species, are absolutely dependent upon southern forest habitats at one time or another in their annual cycle. The importance of bottomland habitats has been recognized by waterfowl managers, and research is getting underway. Woodcock managers should join in this effort and seek ways of including their interests with those of the duck people.

A clear need exists to determine what level of harvest woodcock populations can sustain. Intensive studies on areas such as Moosehorn and Seney National Wildlife refuges can provide the needed information through controlled hunting programs. Such studies also could provide useful information about the vulnerability to hunting of age and sex components of the population, the reliability of wing survey data as a measure of productivity, and other topics of importance to management.

Finally, while I have the opportunity, I want to touch upon a matter of general interest. It has to do with communication. It is well for woodcock researchers to discuss their interests with each other, and symposia such as this provide a useful forum. However, it also is important that we communicate clearly with administrators, outdoor writers, and the public.

The woodcock has unique characteristics that make it a valuable indicator of environmental health. This should be made widely known among decision makers. One result might be a more sympathetic ear when requests are made for research and management funds.

Some of you know how to manage habitat to increase woodcock productivity and abundance. This information is most useful when it is in the hands of private and corporate interests which control enormous amounts of habitat. And, as all of us know, habitat is the key to woodcock abundance.

I have enjoyed attending this symposium. It has provided a welcomed opportunity to refresh and increase our knowledge about the American woodcock. Thank you for your courteous attention.

WILDLIFE RESEARCH REPORTS

1. An Analysis of the Population Dynamics of Selected Avian Species with special reference to changes during the modern pesticide era, by Charles J. Henny. 1972. 99 pp. illus.
2. Population Ecology of Migratory Birds: Papers from a symposium held at the Migratory Bird Populations Station, Laurel, Maryland 9–10 October 1969. Sponsored by American Institute of Biological Sciences in Cooperation with Bureau of Sport Fisheries and Wildlife, United States Department of the Interior. 1972. 278 pp. illus.
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